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ILLUSTRATIONS OF FUNGI—XIV

William A. Murrill

The accompanying plate represents the two most poisonous species of fungi in this region, commonly known as *Amanita phalloides* and *Amanita muscaria.* Certain related species are also represented.

For a discussion of the principal species of this genus occurring in eastern North America, see Mycologia for March, 1913. The poisonous species of this group are discussed in Mycologia for November, 1910.

Venenarius phalloides (Fries) Murrill

Amanita phalloides Fries

Deadly Amanita. Destroying Angel

Plate 87. Figure 1. ×1

Pileus convex or campanulate to expanded, 3–15 cm. broad; surface smooth, slightly viscid when moist, glabrous or decorated with scattered patches of the volva, varying in color from pure-white to yellow, yellowish-green, green, gray, brown, or blackish, margin rarely striate; context extremely poisonous, white, not objectionable to the taste but having at times a somewhat disagreeable odor; lamellae white, unchanging, broad, ventricose, rounded at the base and free or adnexed; spores globose, smooth, hyaline, 7–10 μ; stipe subequal, bulbous, long, smooth or floccose-scaly, usually white, stuffed or hollow, 6–15 cm. long, 0.5–1.5 cm. thick; annulus superior, membranous, thin, ample, persistent or at times becoming torn away, usually white; volva white, adnate

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to the base of the large, rounded bulb, the limb usually free, conspicuous, lobed, thick and fleshy, persistent, but at times breaking partly or wholly into irregular patches that are either carried up on the surface of the pileus or remain at the base of the stipe.

This most deadly species of all the fleshy fungi has been often described at length. The reader is referred to MYCOLOGIA for November, 1909, for a discussion of its poisonous properties. The variety of colors assumed by this species—white, yellow, green, gray, brown, blackish—and the fact that the annulus and the limb of the volva may sometimes be lost make it necessary to use great caution in selecting any white-gilled species with bulbous stipe for food, whether an annulus is present or not. All species of *Venenarius* and *Vaginata,* and several species of *Lepiota* must be examined with great care.

Vaginata agglutinata (Berk. & Curt.) O. Kuntze

Amanitopsis volvata (Peck) Sacc.

LARGE-SHEATHED VAGINATA

Plate 87. Figure 2. ×1 .

Pileus hemispheric to plane, sometimes slightly depressed, very variable in size, 2–8 cm. broad; surface dull-white or yellowish, rarely reddish-brown at the center or entirely reddish-brown, pulverulent, floccose-squamose, or with large volval patches; lamellae free, rounded behind, broad, crowded, white; spores ellipsoid, smooth, hyaline, $10-12 \times 6-7\,\mu$; stipe very variable in size, 1–7 cm. long, 3–8 mm. thick, equal or tapering upward, enlarged at the base, whitish, minutely floccose-squamose, stuffed or solid; volva unusually large, firm, membranous, persistent, more or less lobed.

Venenarius muscarius (L.) Earle

Amanita muscaria (L.) Pers.

FLY AMANITA. FLY AGARIC. FLY POISON

Plate 87. Figure 3. ×1

Pileus globose to convex, at length nearly plane, 8–20 cm. broad; surface slightly viscid when fresh, red or orange to yellow, rarely paler, adorned with numerous whitish or yellowish warts, margin slightly striate; context white, yellow under the pellicle, extremely poisonous; lamellae white, rarely pale-yellow-

ish, rather broad; reaching the stipe and forming slight decurrent lines upon it; spores subglobose to ellipsoid, $9–10 \times 7–8\,\mu$; stipe subequal, white or pale-yellowish, stuffed or hollow, usually rough with concentric, margined scales adnate to the bulbous base, 8–25 cm. long, 2–3 cm. thick; annulus superior, large, membranous, persistent, white; volva white or yellowish, usually entirely fragile, rarely slightly margining the bulb.

This widely distributed and very dangerous species has several color forms, and it has often been confused with edible species. Its poisonous properties and the use of atropine as an antidote have been considered in previous papers.

Venenarius flavorubescens (Atk.) Murrill

Amanita flavorubescens Atk.

VELVET-STEMMED AMANITA

Plate 87. Figures 4 and 7. $\times 1$

Pileus convex to expanded, scattered or gregarious, sometimes subcespitose, 6–10 cm. broad; surface flavous with a melleous tint to dark-brownish-melleous, usually darker at the center, adorned with yellow or brownish-yellow, floccose patches which may persist or partly disappear with age, margin faintly striate, usually paler; context thin, yellowish; lamellae free to adnexed, not crowded, oblong-elliptic in outline, white, much resembling those of *V. rubens* when dry; spores globose to ellipsoid, smooth, hyaline, $8–10 \times 5–8\,\mu$; stipe subequal or tapering upward, usually somewhat enlarged below, but scarcely bulbous, fibrillose or floccose-mealy, at times conspicuously roughened, characteristically tomentose when dry, concolorous or paler above, reddish below, turning slowly to red at the base when bruised, 5–12 cm. long, 5–12 mm. thick; annulus ample, membranous, persistent, flavous; volva flavous or nearly so, friable, the fragments remaining on the surface of the pileus and at the base of the stipe or disappearing according to weather conditions.

The two figures show striking differences in color and form, but the species is a variable one. Figure 4 represents the dark form; figure 7 the normal yellow form with an unusually rough stipe.

Venenarius Frostianus (Peck) Murrill

Amanita Frostiana Peck

FROST'S AMANITA

Plate 87. Figure 5. ×1

Pileus thin, convex to expanded, plane or slightly umbonate, 3–8 cm. broad; surface viscid, adorned with floccose, yellow fragments of the volva, often becoming entirely glabrous, chrome-yellow to orange-yellow, slightly darker in the center, margin smooth or slightly striate; lamellae free, rounded at both ends, subdistant, white or yellowish; spores globose or ovoid, smooth, hyaline, 6–10 μ long; stipe slightly tapering upward from the bulbous base, white or yellowish, smooth, flocculose, stuffed, 6–13 cm. long, 0.4–1.5 cm. thick; annulus membranous, delicate, easily torn away, pale-yellow to chrome-yellow; volva yellowish, usually entirely friable, rarely slightly margining the bulb.

A beautiful species resembling *V. muscarius,* but smaller and more slender and not poisonous.

Venenarius cothurnatus (Atk.) Murrill

Amanita cothurnata Atk.

BOOTED AMANITA

Plate 87. Figure 6. ×1

Pileus globose to convex, at length expanded, 3–7 cm. broad; surface quite viscid when moist, decorated with small, scattered, soft, floccose warts, white or tinged with lemon-yellow, or with the center tawny-olive, even or finely striate on the margin; context white, without odor; lamellae rounded behind, crowded, plane, white; spores globose, smooth, hyaline, 7–9 μ; stipe cylindric, bulbous, flocculose or floccose-scaly, white, hollow or rarely stuffed, 5–12 cm. long, 0.4–1 cm. thick; annulus white, thick, persistent, volva white, adnate to the large, ovoid bulb, circumscissile, breaking uniformly and leaving an abrupt ring at the top of the bulb.

The annulus was very low in the specimen figured and the boot very short. The pileus was also less viscid and somewhat different in color from plants found commonly farther south.

NEW YORK BOTANICAL GARDEN.

THE NATURE AND CLASSIFICATION OF LICHENS—II. THE LICHEN AND ITS ALGAL HOST[1]

Bruce Fink

The writer had no thought, in addressing the questionnaire to botanists three years ago, of attempting to settle thus the classification of lichens. It was thought rather that the views of leading botanists would be valuable, and also that the problems involved could be treated more intelligently after current opinion and the arguments back of it were known. As stated in the first paper of this series, the writer has reserved his own ideas for this paper and another to follow in the series. *Since his views regarding lichens are not those held by most persons who have worked on these plants, the phraseology used, even in the discussions of researches, must be somewhat different from that found in the papers cited. If the facts appear, to those whose writings are considered, to be distorted, careful analysis will probably show that there is no other distortion than that necessarily involved in treatment under a different conception of the nature of the lichen.*

The Presence of Algae in Lichens Established

For centuries lichens and the algae which grow with them were thought to be genetically related. Walroth (137), in the first account of the green cells in lichens, noted their resemblance to certain algae. Elias Fries (60), Kützing (78), Koerber (73, 74), Nägeli (93), Thwaites (129), Thuret (128), Tulasne (136) and Itzigsohn (68) renewed the observations of Wallroth. Some of these and others as Sachs (108), Hicks (67), Nylander (95, 96), Krempelhuber (76), Müller (91) and Arcangeli (2) thought that the algae were the primordia of certain lichens or other stages in their development. Several observers as Bayrhoffer (18), Müller (90, 92), Th. M. Fries (61), Archer (3), Arcangeli (2),

[1] Contributions from the Botanical Laboratory of Miami University—X.

Crombie (41) and Minks (85) committed themselves to the view that the algae arose from the ends of the lichen hyphae.

De Bary (15), and Schwendener (118) more confidently, declared that lichens and certain algae grow together in such intimate relationship as to be long considered parts of the same plant. In spite of the researches of Bonnier (27, 28, 29, 30, 31), Baranetsky (14), Bornet (32, 33), de Bary (15), Famintzin (53, 54), Möller (87, 88), Reess (102), Schwendener (116, 118, 119, 120, 121), Treub (135) and Woronine (144), the European lichenists of that day, as Crombie (40, 41, 42), Th. M. Fries (61), Krempelhuber (76, 77), Minks (85), Müller (92), Koerber (75), Lindsay (83) and Nylander (96, 97) failed to believe that the green cells in lichens are really algae.

With the passing of these men and the coming of a generation of lichenists who agree with other botanists regarding the presence of algae in lichen thalli, it might be supposed that there could not be at present any question regarding the nature and the proper treatment of lichens. However, the only matter thoroughly settled is that the green or the blue-green cells in lichens are algae.

CONSIDERATIONS OF RECENT VIEWS AND ARGUMENTS OF BOTANISTS

We have been slower to reach an agreement regarding the nature and the proper treatment of lichens than were earlier botanists to find the truth concerning the algae that grow with these plants. True, some botanists have settled the questions involved to their own satisfaction, and others hold a tentative opinion. Advocates of certain ideas regarding lichens have stated, at different times, that their views on the subject were those generally held by the botanical world; but these views have proved, as a result of the statistical study given in the first paper of this series (55), not to be held by a majority of botanists. Moreover, majorities, even of scientific men, are not always right; and we may inquire whether the consensus recently expressed regarding lichens is final. In order to reach a safe conclusion, it has been necessary to review a large portion of the literature of lichenology to ascertain what is valuable for our purpose.

Many botanists were asked, two years ago, to express themselves regarding the classification of lichens, and the results of the correspondence have appeared in MYCOLOGIA (55) for September, 1911. It was supposed that those who replied would deem it necessary, in sustaining their views regarding classification, to state clearly their ideas concerning the more fundamental problem of the nature of lichens. Of the 42 replies quoted, 10 contain no words from which any inference can be drawn concerning the nature of these plants. The other 32 replies touch the matter, for most part, in an obscure manner, often by inference rather than word. This must be taken to mean that those who wrote, with few exceptions, regard the question of the nature of the lichen settled. We may well inquire, then, what these modern botanists said concerning this matter, by word or by reasonably safe inference. Ten of them said nothing. Fourteen stated in more or less certain fashion that lichens are fungi, and 18 appear to believe that lichens are colonies of algae and fungi, or dual organisms. This result, surprising as it is, demonstrates that some form of the dual hypothesis is still much alive, at least in the phraseology used by botanists in writing about lichens, and that the much discussed and vexing problem of the nature of lichens is by no means settled.

In the present condition of affairs, it is difficult for most botanists to write a full page about lichens without contradicting any position taken, unless it be one not far removed from the traditions regarding these plants. As a whole, the replies quoted in MYCOLOGIA are as consistent as anything that has appeared on the subject; yet it would be rash for one who has examined the statements carefully to assume that he is certain that all of these botanists said what they intended. Indeed, some of the replies say that lichens are dual organisms, but should be distributed among fungi. Those who replied thus either believe that lichens are fungi, or that the fungi of the dual organisms should be distributed. But they said neither of these things. One botanist who believes that the lichen is a fungus said positively in his reply that it is a dual organism. A few committed the too common inconsistency of stating that lichens are both dual organisms

and fungi. Of course, these errors of statement result largely from clinging to the traditional phraseology.

TEXT-BOOK TREATMENTS OF LICHENS

Writers of text-books on plant morphology have, with a few notable exceptions, signally failed to be consistent in their treatment of lichens. The 1908 edition of the Strasburger (126) text says on page 348: "Lichens are symbiotic organisms; they consist of filamentous fungi, usually *Ascomycetes,* rarely *Basidiomycetes,* which live in intimate relationship with unicellular or filamentous algae, *Cyanophyceae* or *Chlorophyceae,* and together with these, form a compound thallus or consortium." ("Die Flechten sind symbiotische Organismen, sie bestehen aus Fadenpilzen und zwar aus *Ascomyceten,* nur in ganz vereinzelten Fällen aus *Basidiomyceten,* welche mit einzelligen oder fädigen Algen, *Cyanophyceen* oder *Chlorophyceen,* gemeinsam vegetieren und so einen zusammengesetzen Thallus, ein Konsortium bilden.") This expresses clearly the peculiar idea that the lichen is a fungus and that the consortium is the lichen plus the alga with which it is associated. But the next sentence reads thus: "The lichen-fungi and the lichen-algae should, in a natural system, be classified with the nearest related fungi and algae." (Die Flechtenpilze und Flechtenalgen sind im natürlichen System in die gruppen der nächstverwandten Pilze und Algen einzureihen.) This contradicts the first statement and indicates that the intention was to regard the lichen as a consortium. Fortunately, Lang has corrected the inconsistent statement in the English edition, but the German student still meets this incoherent treatment in his leading text-book.

The Warming-Potter (139) text of 1895 says: "The lichens are fungi . . . which have entered into a peculiar symbiotic relationship with algae." This is coherent and easily understood. But a little below the authors say, "The fungus forms the largest portion of the lichen"; and one wonders how it is, if the lichen is a fungus, as stated in the first quotation, that it does not, as stated in the second, form all of itself. The Curtis (45) text of 1907 has this statement: "The lichen is one of the most remark-

able plants in the vegetable kingdom, since it is the union of two separate plants, a fungus and an alga" (see also 44). This doubtful and confusing statement is left with little explanation, and the author of the book reaches the remarkable conclusion that since "the fungus forms the bulk of the lichen," lichens should be regarded as fungi. The inconsistency of this statement needs only to be pointed out, and yet similar treatment is often found in text-books and elsewhere. The Bergen and Davis text (21) has it thus of lichens: "They are not single plants, but composite organisms made up of algae which are contained in an enveloping mesh of fungal filaments." This plainly makes the lichen a group of algae, though the authors had no intention of saying so remarkable a thing. The Bessey (22) text of 1906 is coherently correct, and the Bergen and Caldwell (20) text of 1911 is quite as coherently incorrect regarding the nature of lichens. These are fair samples of treatment of lichens in texts of general botany.

Writers of texts on plant physiology have held nearer to the traditions concerning lichens and, consequently, have usually made more coherent statements, which have been almost uniformly incorrect.

On the whole, we can not regard the fundamentals of the lichen question settled so long as such confusing, incoherent and erroneous utterances continue to emanate from leading botanists.

RECENT EXPRESSIONS REGARDING THE NATURE OF LICHENS

We are still concerned primarily with the problem of the nature of the lichen and its relation to the algal host. The classification of lichens must be treated last of all, and can not be reached in this paper. Bessey (23, 24, 25, 26) and Clements (35, 37) have expressed themselves to the effect that lichens are fungi and should be distributed to the exclusion of the group Lichenes. Reinke (105, 106) and Schneider (109, 110, 111, 112, 113), at the same time, have been stating at greater length that lichens are distinct from all other plants. When we have finally decided which side of the controversy is in accord with the facts established by research and are able to follow the conclusions reached in a logical manner, we may regard the problem of the nature and the proper treatment of lichens settled.

Reinke, Schneider, and other advocates of consortism, as is well known, regard the relation of the lichen to the alga with which it grows so intimate and mutualistic that the plants growing together must be considered collectively as an individual. It is not deemed essential to the hypothesis that both symbionts should be equally benefited by the association; nor is it regarded necessary that the relation should be beneficial to both symbionts in all respects. It is said by its adherents to be important for the hypothesis that each member should be aided more than injured by the symbiosis, so that the final outcome is advantage to both. Added to this is the intimate union of the two symbionts into what appeared, until de Bary and Schwendener proved otherwise, to be a veritable morphological unit. According to the hypothesis, only one of the symbionts need be wholly dependent upon the other, in order that a new individual may be formed with morphological and physiological characters quite distinct. The other symbiont may be able to live outside the association. The fact established by Frank (58) that certain lower lichens can and do usually exist during a large part of their life outside the relationship with algae is overlooked, and we are given also the contrary statement that the fungus does not and never has existed as such free in nature. It is claimed that the algae found in lichens are more difficult to cultivate than free algae; and this is said to indicate that the algae of these symbiotic associations will in time become as dependent upon the symbiotic relationship as are the fungi now, except perhaps in the lowest lichens. So it is supposed that the relation is becoming closer and closer, and that finally it will be so intimate that neither symbiont will be able to live independently. Then will the individualism be perfect according to the hypothesis. This erroneous hypothesis is refuted by certain considerations to follow in this paper.

The term "consortium" was proposed for the peculiar relation of lichens to algae by Reinke (65, 104, 105), at the suggestion of Grisebach, and was adopted by de Bary (16), who advocated mutualism and individualism, though he seems to have repudiated both later. Recent views expressed by Artari (5, 6), Schneider (109, 110, 111, 112, 114), Peirce (98, 99), Elenkin

(49, 50), Treboux (122), Famintzin (52) and Danilov (46), with the recent enlargement of Reinke (105, 106) upon his original statement, place before us several interesting hypotheses regarding the relation of the lichen to the alga which lives with it. We shall revert to some of these researches toward the close of this paper. Suffice it to state here that Elenkin's hypothesis of endosaprophytism and Danilov's and Peirce's views of parasitism of the lichen upon the alga are quite opposed to the hypotheses of Reinke and Schneider or the more extreme views of Famintzin. In short, the evidence furnished by recent investigation is, as a whole, against all hypotheses of individualism or mutualism. However, granting for the moment, that the relationship is thoroughly mutualistic; that the statement that neither symbiont can live alone, disproved as it is by the cultures of Bonnier (31), Bornet (32), Möller (87, 88) and others, is true; and that the hinted suggestion of Famintzin (52) that the chlorophyll granules of higher plants resemble certain algae and may be such is also proved, some of us would not even then believe the individualism hypothesis to be tenable.

Should such an improbable thing as proving the chlorophyll granules to be veritable algae which could not exist outside the tissue of higher plants come to pass, the writer at least would be disposed to regard these structures, which would not then be genetically related to the plants in which they occur, not parts of the plants, but foreign to them. In short, neither the present relation of the lichen to its symbiotic alga nor any mutualistic relation that may possibly come to pass in the future seems to constitute individualism in any true sense.

It seems remarkable that Danilov (46), Elenkin (49, 50) and Peirce (98, 99, 100) could favor parasitism or saprophytism of lichens upon the algae, and still believe in the dual-nature hypothesis. It will be pointed out below that de Bary did the same in his text-book, and this unreasonable position can be due to nothing else than blindly adhering to the traditions regarding the nature of lichens.

Those who believe that lichens are fungi have not made long arguments for their view. Their efforts have necessarily been

directed mainly toward refutations of mutualism, consortism and individualism; and it is true that lichens resemble other fungi so strongly that there can be no reasonable doubt, once the dual hypothesis is disproved. The best presentation is that of Clements (35). This writer has avoided the inconsistencies so commonly committed by those who treat lichens as fungi, and has given a strong refutation of the consortism hypothesis of Reinke. He also incidentally makes plain, in the paper cited, his views regarding the nature of lichens and their classification. Besides Clements' paper, some of the last 14 quotations in MYCOLOGIA (55) are strong arguments. These are directed mainly toward the less fundamental matter of the distribution of lichens, a consideration barely touched in Clements' paper.

One reads sometimes of the arguments of de Bary and Schwendener for the fungal-nature view, but these men never believed that lichens are fungi. On looking through the 1884 edition of his text-book, one finds that de Bary (17) took the remarkable position that the fungus is parasitic on the alga, but that both are none the less parts of the lichen. His earlier views noted above, in which he recognized consortism, though incorrect, are more tenable. Probably Schwendener's paper of 1873 (121), more than any of his other articles, has caused some botanists to suppose that he regarded lichens as fungi. Indeed, the title would render any other position untenable for him; but, while he maintains that the chlorophyllous cells are algae, wherever he commits himself in the paper, he makes these algae parts of the lichen.

REASONS FOR REGARDING LICHENS AS FUNGI

The main arguments of those who believe that lichens are fungi, so far as they relate to the nature of the lichen rather than to classification, are as follows. The luxuriant growth and the rapid multiplication of algal cells within a lichen are not due to mutualistic relation with the lichen, but rather to some condition of parasitism, perhaps hypernutrition caused by irritation. It is pointed out that the vegetative structure and the fruits of lichens are similar to those of other Ascomycetes. It is said further that phylogenetic and morphological continuity is

apparent enough between *Thelophora* and *Cora*-like lichens, where we have the process of the evolution of new lichen phyla going on before our eyes, and also in the relationship of *Graphis* to *Hysterium, Calicium* to *Mycocalicium, Bilimbia* to *Mycobilimbia, Basidia* to *Mycobacidia, Lecidea* to *Patinella,* etc. It may be added here that the recent papers by Acton (1), Lagerheim (79), Schneider (114), de Seynes (122, 123), Zukal (151) and others add to the evidence through the discovery of many lichens in the making. These researches are considered at length below.

The arguments of those who believe that lichens are fungi seem perfectly tenable, but close analysis is necessary. For the writer at least, it matters not whether the relation of the lichen to the alga is parasitism, saprophytism, or mutualism, even of the type that is believed by some botanists to be the acme of individualism, for it seems reasonable to him to regard the lichen a fungus if the relation is the most mutual possible as well as if it is antagonistic. But the problem arises whether it is consistent to regard the lichen a fungus, since in so doing we are ignoring part of that which was originally considered a portion of the lichen, viz., the symbiotic alga. The zoölogists do not regard zoöchlorellae a part of *Hydra viridis,* fresh water sponges, or other animals in which they occur. Though the symbiotic relation of the lichen to the alga is different from that of the hydra or the sponge to the alga found within it, and though the alga may sometimes form a larger portion of the symbiotic colony than does the lichen, congruity demands excluding the alga from our conception of the lichen.

It has been suggested that the term lichen should be given over to plant physiologists and ecologists, to signify a colony of special interest to them. There are at least two difficulties with this proposition. The first is that most botanists will continue to use the term lichen for purposes of taxonomy and morphology, in spite of any suggestions that might be made, and the second is that relegating the term to workers in certain fields of botanical work would not be the best solution, were it feasible. After studying the literature of lichen physiology and ecology carefully, it does not appear best for physiologists and ecologists to depart from the usual method and consider colonies rather than individ-

uals. Ecological and physiological studies of the lichen and the alga with which it lives are just as interesting and more comprehensible when these plants are considered in their proper relation as independent but intimately associated organisms. Furthermore, this method in plant physiology and ecology would aid in bringing botanists into general accord as to method of treating these plants, and would thereby help do away with the inconsistency and confusion which make it so difficult for botanists to express themselves in a coherent manner regarding lichens. The physiologists and the ecologists have been less inclined than taxonomists to depart from the traditions concerning lichens; but they may well ponder carefully the latest views of leading lichenists (55), who are as much disposed to think that lichens are fungi as are other morphologists and taxonomists. The one argument in recent years for not considering the lichen a fungus pure and simple has been the supposed mutualistic relation of the lichen to the alga, and this has been made to appear untenable by the recent researches of Danilov, Elenkin, Peirce and others cited above. In view of these investigations, it would seem that plant physiologists and ecologists, especially, should abandon the dual hypothesis, which is not tenable in any form or under any condition of mutualism and is wholly unreasonable if it is admitted that the relation of the lichen to the alga is antagonistic. The researches bearing on this problem are considered at length toward the close of this paper.

DIFFICULTIES TO BE MET IN TREATING LICHENS AS FUNGI

Plainly, the only consistent view is that the lichen is a fungus. But having reached this position, there is difficulty enough for mycologists, especially those that study Ascomycetes, to which the lichens very largely belong. Botanists seem, as a rule, to think that the relationships of lichens to other Ascomycetes should be ascertained by lichenists, while students of non-algicolous Ascomycetes, trained as badly in this matter as are the lichenists, continue to avoid the study of algicolous Ascomycetes. This position seems wholly unreasonable. If we are ever to know the relationships of algicolous to non-algicolous Ascomycetes, lines of cleavage in study must cease to be determined by the food habits of

these plants. Forms that appear to be closely related must be studied together, whether all are algicolous, all non-algicolous, or part of them one and part the other. Nor is it necessary that one worker should attempt to study all Ascomycetes, except in a very general way.

Another difficulty is that lichen descriptions have usually been based upon the assumption that the alga forms part of the lichen. Lichenists, even those who believe that lichens are fungi, still for most part continue to give, in their descriptions, details regarding the size and the form of the algae enclosed within lichen thalli. Statements regarding the algae should not be given as a part of descriptions of species, genera, or larger groups of lichens, but should follow or precede the descriptions. The changes needed are greatest in those lichens which grow throughout the algal colonies. The well known *Collema pulposum* (Bernh.) Ach. will serve as an illustration. The thallus has been described hitherto as orbicular or irregular, middle-sized, very gelatinous when wet, frequently showing a rosulate arrangement of the lobes, rather thick especially toward the center, leek-green, olivaceous or blackening, the lobes repand-crenate, etc. This is mainly a description of the algal colony in which the lichen is imbedded. The lichen thallus should be described somewhat as follows: thallus a loose network of hyaline, septate, branching hyphae, which are 2.5 to 4 mic. in diameter, with cells 15 to 30 mic. long; simple rhizoids hyaline to light brown, with cells 4 to 5.5 mic. in diameter and 20 to 25 mic. long. Then may follow a description of the sexual reproductive organs and of the apothecium and its parts. Following this the algal colony in which the lichen grows may be described in a separate paragraph. The description of the Collemaceae as a whole and all the genera and species will need to be modified in similar fashion. What are specific and what are generic characters will appear in the revision. What species will have to be abandoned because of excluding from the descriptions the characters which belong to the algal hosts can only be ascertained by critical study.

The changes required in the descriptions of those lichens which contain the symbiotic algae in a stratum within their thalli will not be so great, and fortunately these lichens are far more numerous

than those in which the lichen ramifies throughout the algal colony. More difficulty will probably appear in the crustose than in the foliose and the fruticose species. In the descriptions of many genera and species of lichens, the only changes needed are to remove whatever is said of the algae from the descriptions and to modify in some manner the statements regarding the so-called algal layer and the soredia. In thalli which contain the algae in a definite stratum, the algal layer may well be called the *haustorial layer.* This has the advantage of excluding from the statement an organism which does not belong to the lichen. The soredium should be regarded as *a tangled mass of lichen hyphae and haustoria.*

Perhaps few botanists had thought that so great changes in the treatment of lichens and consequent difficulties in using the literature of lichenology were involved, unless these plants were distributed to the exclusion of the group Lichenes. The trouble really appears when we consider lichens properly as fungi, whether we distribute them or not; though the less fundamental matter of distribution does offer even more intricate problems. Treating together as colonies the lichens and the algae which occur with them and continuing to describe and classify these colonies is the only way to avoid the enormous amount of labor involved in revision. This is, of course, wholly illogical, and the only consistent course is to break with past methods and treat lichens rightly, regardless of the difficulties which present themselves.

THE BIOLOGICAL RELATIONS OF CERTAIN LOWER LICHENS

By considering carefully some lower lichens and some plants that may not be lichens, we will be able to gain information regarding the relation of lichens to their algal hosts and to other fungi. Those who hold to some form of dual hypothesis insist that these lower and doubtful lichens are atypical and should not be considered; but the largest groups of lichens are among the lowest forms. Hence, the lowest lichens are interesting and instructive in consideration of problems relating to the nature and the disposition of these plants in general. Their study throws light upon phases of the problem which can scarcely be under-

stood so long as we confine attention to the higher foliose or fruticose lichins or even to higher crustose forms.

De Seynes (122, 123) found specimens of *Sclerotinia tuberosa* (Hedw.) Fuck., the hymenial surface of which showed produced ends of paraphyses closely applied to unicellular algae. The results were fully published in 1886, and the figures show that in some instances branching, haustorial elongations of three or more paraphyses are closely attached to a single algal cell. The alga is said to be *Chlorococcum humicola,* which occurs with lichens so commonly. The swollen and turgid haustoria are cut off by a septum and are like those of typical lichens which live with the same alga. But few of the paraphyses are attached to the algal cells. This observation has not been repeated, and the relation of this fungus to the alga is rare and accidental; yet it illustrates the manner in which lichens arose from non-algicolous fungi. Our view of lichens can be construed to make the rare *Sclerotinia* individual which lives with the alga a lichen; but this may better be left to personal judgment. The point regarding the origin of lichens and their relationship to other fungi is as well shown whether we regard these individuals lichens or not.

Archer (3) described and figured lichen apothecia on *Scytonema myochrous, Sirosiphon alpinus, S. pulvinatus* and *Stigonema mamillosum.* The spores are much alike in all of these and strongly resemble those of our *Ephebe pubescens* (L.), Fr., though not the same. He thought perhaps that the lichen was the same on all of these algae, but his spore measurements would indicate otherwise. He found neither hyphae nor sexual organs; but it is very probable that he observed one or more primitive, facultative lichens.

Frank (58) found that *Arthonia radiata* (Pers.) Ach. grows within the periderm of trees, often for years, wholly outside the relation with the symbiotic alga, *Trentepohlia umbrina,* and that some individuals never parasitize the algal host at all. After a time, according to Frank, some of the algae bore into the periderm and are attacked by the lichen, which now grows more luxuriantly, penetrates deeper into the periderm, becomes also partly superficial and produces apothecia. Those individuals that fail to enter into the partnership with the alga do not produce apothe-

cia. Thus it appears that these fungi can live without the algae, but are benefited by the association with them. *Trentepohlia* is known to live commonly in the periderm. Therefore, it seems certain that this alga is often there and enters into the hostal relation with the lichen soon after the lichen spore germinates and penetrates the periderm, though Frank seems to have supposed that these lichens were always independent of the alga during a good portion of their course. More of Frank's results are given toward the close of this paper.

Lindau (81) accepted, in the main, the conclusions of Frank and passed on to a profitable consideration of the same or similar lichens and the algae which grow with them. He found *Trentepohlia* filaments on the surface of the bark entwined by hyphae of *Arthopyrenia punctiformis* (Pers.) Mass.; but the portion of the fungus within the periderm was wholly free from the algal filaments. He concludes that this *Arthopyrenia* lives without other than an accidental relation with the alga.

These researches are interesting and instructive in many ways. Frank decided that typical lichens are Ascomycetes which live in symbiotic relationship with algae; but he regarded all of these plants which belong to the same genus lichens, whether all or only part of them live with the algae. Lindau, on the other hand thinks that those that live outside the symbiotic relation are not lichens. These studies also indicate that the lichen is benefited by the association with the alga quite as plainly as do the cultural experiments with higher lichens; and this makes sure the position that those fungi which live during all or part of their life in parasitic relation with algal hosts are lichens, provided that they sustain, at the same time, the usual relation with an external substratum. Lindau thinks the *Arthopyrenia* considered above is not a lichen, since the alga does not grow more luxuriantly because of association with it. We can not accept this view, but believe that the fungus is a lichen if it is benefited by the association with the alga instead of using it merely as a support about which to twine. We agree with Lindau that those species which do not enter into parasitic relation with algae are not lichens, even though they belong to the same genus with others that enter into relations beneficial to themselves and are lichens. Whether a fungus

species, some of whose individuals run part of their course in the parasitic relation with an alga, while others pass their whole life outside this relation, is a lichen is a rather fine distinction that is doubtful at best and scarcely worth considering. But it seems more reasonable to say that all species that are better developed when they live with algae than when they do not are lichens.

Zukal (151) published an account of the frequent occurrence of one of the Hypocreaceae with an alga which he thought to be *Palmella botryoides*. He named the fungus *Epigloea bactrospora* Zuk. The perithecia are semi-immersed in the algal colony, through which the hyphae ramify and are attached here and there to the algal cells. We have here a pyreno-lichen, belonging to a well known group of Pyrenomycetes. Hence its phylogeny seems certain enough, and it furnishes another point of approach of lichens to other well known fungi. The lichen is so little modified that Zukal placed it near the genus, *Barya*, of the Hypocreaceae; but Zahlbruckner, in Engler and Prantl (145), has removed it from its natural position and has erected for it a lichen family, the Epigloeaceae. The alga is sometimes found free on mosses, and is in other instances attacked by the lichen. However, the occurrence of free algae growing with those of the same species attacked by lichens is known to be frequent, as will be proved later in this paper.

Zukal (152) also published some interesting results in his paper entitled "Halbflechten." Some of these concern his monotypic genus *Parüphrädria* and the species *Parüphrädria heimerlii* Zuk., found on the leaves of *Jungermannias*. The lichen gains entrance to these hepatics through the rhizoids, which it entwines and penetrates. It extends into the outer tissues of the stems and penetrates the leaves, some of which are finally killed. The apothecia usually occur on the leaves and most commonly at points where algal colonies of *Gloeocapsa* or of *Palmella* happen to be present. Here the lichen hyphae grow through the algal colonies in all directions, but do not penetrate into the algal cells. Microscopic squamules or granules are formed. Zukal considered each of these a lichen thallus. Only a portion of the lichen penetrates into the algal colony; but some parts of lichens are commonly external to the algal mass with which they grow, and

a lichen is a lichen whether this external portion be much or little. We must consider the whole structure, the parts that grow on the hepatic as well as those that grow in the algal mass, a very primitive lichen. The undetermined point of special biological interest regarding the fruiting is whether the apothecia are ever produced before the relation with the alga is established. It matters not that the apothecia are sometimes formed at some distance from the algal colonies, for the nourishment could be carried by the hyphae. In Engler and Prantl, Lindau (82) gets this plant instead of Zahlbruckner, and places it near Bulgaria. Rehm (103) agrees with Lindau regarding the position; but Rehm believes that lichens might well be distributed among other fungi and frequently treats lower lichens with other Ascomycetes. So his stand is not proof that he does not regard this plant a lichen. *Gloeopeziza rehmii* Zuk., another of Zukal's half-lichens (152), produces its apothecia at a distance from the *Gloeocystis* or the *Palmella* masses, into which certain hyphae penetrate and very probably convey nourishment to the points where the apothecia are developing. Zukal says that this lichen passes its early stages as an epiphyte, but not as a parasite, on the leaves of *Jungermannia triophylla;* and it would be especially instructive to know certainly whether the apothecia ever develop before the algal colonies are attacked. Rehm (103) places this lichen with the Bulgariaceae, but Lindau (82) considers it one of the Pezizaceae.

Very different are the conditions in *Nectria phycophila* Zuk., another of Zukal's half-lichens (152), which grows in *Hypheothrix zenkeri,* of the Oscillatoriaceae. The mycelium of the lichen is found in the trichomes of older dead portions of the algal colony; but, in younger portions of the colony, the hyphae occur in the sheaths only. No haustoria were noted; but this fungus, recognized as a *Nectria* by Lindau (82), is as good a lichen as are *Ephebes* or *Collemas* and other lichens in which the relation of the lichen to the alga is not very intimate. One who believes that the lichen consists of the fungus and the alga which grow together can not consistently place this or any lichen with fungi; so this plant can not properly be regarded a *Nectria* by them. Yet, this inconsistency did not occur to Zukal, who regarded the lichen a dual organism; nor does it seem to have troubled many

other mycologists, who treat lichens in general quite as inconsistently. On the other hand, those who believe that lichens are a distinct taxonomic group should, to be consistent, claim this plant, but they have not. The main difficulty disappears when we regard the lichen a fungus. The last difficulty fades for those who maintain that these fungi should not constitute a taxonomic group, but should be distributed in the best manner possible.

Endomyces scytonematum Zuk., the last of Zukal's half-lichens (152), is supposed to be *Ephebe hegetschweileri* Itz. The spores occur in naked clusters of asci, characteristic of the Gymnoascaceae. The lichen hyphae grow for a time in the sheaths of *Scytonema* filaments; but as the asci develop, the hyphae penetrate into the trichomes of the alga, which are soon destroyed. Then follows, of course, the death of the lichen soon after the fruit is produced. Zukal took the position that we have not a lichen in this instance, since the relation is antagonistic and the fungus short lived. But mutualistic symbiosis is surely no *sine qua non* of the lichen and, indeed, seems not to exist at all in those plants. Much less is long life necessary. The early death of the algal host is good proof that the fungus derives benefit from the association with the alga; and the best and, apparently, the only biological criterion for the lichen is that it should live in parasitic relation with an alga and at the same time maintain a relation with some organic or inorganic substratum. According to this standard, we have here a lichen which plainly belongs to the Gymnoascaceae. Of course, it should be left in this group, instead of artificially placing it elsewhere; but in order to do so, it is not necessary to deny its being a lichen.

Tobler (132) investigated a few of the several hundred parasites on lichens. Among these *Karschia destructans* Tobler is described from the thallus of *Chaenotheca chrysocephala* (Turn.) Th. Fr. The *Karschia* penetrates into and through the crustose thallus of the *Chaenotheca,* into the bark on which the latter lichen grows. In passing through the lichen thallus, the *Karschia* hyphae attack and kill the *Chaenotheca* hyphae and the alga which grows in symbiotic relation with them. This gives the *Karschia* a parasitic relationship with the *Chaenotheca,* and with the alga, and a saprophytic relation with the bark and perhaps

with the algal cells after these have been killed. The fruit is produced after the saprophytic relation is established. The relations of the *Karschia* to living and dead sources of food supply are certainly complex enough; but we must conclude that the fungus is as good a lichen as are many other fungi which live in relation with algae during part of their life period only.

Similar are the results of Zopf (146), who studied *Rhymbocarpus punctiformis* Zopf on *Rhizocarpon geographicum* (L.) Lam. and *Conida punctatella* (Nyl.) Zopf and *C. rubescens* Arn. on *Rhizocarpon alboatrum* (Hoffm.) Th. Fr. The *Rhymbocarpus* and both *Conidas* enter into parasitic relationship with the algal hosts within the *Rhizocarpons,* and therefore Zopf very properly regarded them low forms of lichens. He concluded that many other parasites on lichens are likewise primitive lichens.

Elizabeth Acton (1) investigated *Botrydina vulgaris* Breb., growing on mosses and hepatics. The minute colonies, barely visible to the eye, cover the stems and leaves, often so thickly as to conceal them. The sheaths of the globular or irregular colonies are traversed by fungal hyphae. On close examination, these sheaths appear to be cellular. In some cultures, Miss Acton obtained a rich development of fungal hyphae and in others small unicellular algae, the results depending upon the kind of medium used or the conditions under which the cultures grew. The sheaths are very resistant to chemicals and are probably composed of fungus-cellulose. In early stages of development, she found fungal hyphae in contact with the sheaths and concluded that the sheaths develop from the hyphae. Sections showed plainly the plectenchymatous nature of the sheaths and the distorted forms of the algal cells. In one specimen, the fungus was intact, but no algal cells could be detected. The alga was also found free. The fungus is doubtless a lichen, living in parasitic relation with a unicellular alga. The alga is *Coccomyxa subellipsoidea,* of the Palmellaceae; and the lichen, on account of the occurrence of ring-like structures similar to the conidia of the Mucidineae, division Helicosporeae, is supposed to belong to that group. Of course this makes what has been known as *Botrydina vulgaris* Breb. not an alga at all, but a lichen parasitic on an alga. The lichen must be renamed as soon as its nature can be ascertained.

Thus far we have been considering ascomycetous lichens. We may now give attention to a few Basidiomycetes, some of which are lichens while the others may be. Möller (89) found a *Cora*-like thelephore growing abundantly with *Cora*. The two plants are alike in structure as well as in macroscopic appearance. He pulverized portions of *Cora* in water and poured the broth over the thelephores. In three months, *Cora* lobes, bearing the alga characteristic of this lichen, appeared along the margins of the thelephore pilei. Microscopic examination proved that the hyphae of the young *Cora* lobes were continuous with those of the thelephores on which they grew. Thus, by field cultures, Möller transformed part of a thelephore into the lichen, *Cora*. The conclusion is that *Cora* is a primitive lichen, growing beside its non-lichen progenitor, the thelephore. The experiments were extended to *Dictyonema* and *Laudatea* as is explained below in the statement under culture experiments.

Lagerheim (79) published a new subspecies of *Stichococcus bacillaris,* which he found growing on *Polyporus lucidus, Trametes pini* and *Daedalea quercina.* He states that his subspecies *fungicola* is similar to *Stichococcus bacillaris,* found growing with some of the Caliciaceae. He makes no suggestion that the fungi on which his alga grows may be lichens in the making. But there is a possibility that such is the case, and that we have here and in other hymenomycetes upon which algae are frequently seen, very primitive lichens, or at least accidental and indifferent associations of algae with fungi which may become lichens in time.

Morgan (86) noted the constant occurrence of *Clavaria mucida* with *Chlorococcum humicola.* Coker (38) observed the same relation of the alga to the fungus. On examination, he found that the hyphae ramify through the algal masses. There are no haustoria, and he regards the relation of the fungus to the alga about the same as that of *Collema* to the *Nostoc* colonies in which it grows. The relation is almost certainly advantageous to the fungus, and Coker's conclusion that *Clavaria mucida* is probably becoming a basidiomycetous lichen seems reasonable.

We may now pass to some unknown fungi which may be lichens. Schneider (114) investigated the relationship of *Trentepohlia aurea* to some unknown fungus. He found the fungal

hyphae closely applied to all of the *Trentepohlia* filaments examined, forming a delicate, reticulated, spirally wound network of hyphal tissue, entwining the filaments from the base to the apex and extending a short distance beyond. This fungus is probably a primitive and imperfect lichen, the fruit of which is unknown. Of course, it is possible that the fungus bears no nutritional relation to the alga, but merely uses it as a support, on which to climb. If so, the fungus is not a lichen; but this supposition is improbable.

One sometimes finds *Sirosiphon* filaments attacked by other fungal hyphae than those of *Ephebe*. These hyphae are usually external, while those of *Ephebe* ramify through the algal filaments. These superficial hyphae bear somewhat the same relation to *Sirosiphon* as do those found by Schneider to *Trentepohlia aurea*, and they may represent some unknown lichen or lichens. The findings of Archer, given above, may well be recalled here.

Many botanists have not known that the transitional forms connecting lichens with other fungi are numerous; but among the Graphidaceae, the Arthoniaceae, other families of lower lichens and the fungi parasitic on lichens are hundreds and probably thousands of species whose biological position can only be known by careful research. Besides these, there are doubtless many more accidental associations of fungi and algae yet to be discovered. In view of these facts, the bridges connecting lichens with other fungi seem to be very numerous.

Whether a given fungus is a lichen is of little, if any, biological importance, and is certainly of no taxonomic importance for those who believe that lichens should be distributed to the exclusion of the group Lichenes. But the biological relationship between fungus and alga is an important one, and the fungi which are partners in it will continue to be known as lichens. Hence, from a biological point of view, it is important to reach some conclusion touching what constitutes a lichen. However, the main object of this discussion is to bring to light some of the very close but little known relationships of plants on the border line between lichens and other fungi. One may regard these as lichens or not. The relationship remains the same in either case, and research must discover many more such relationships before our knowledge of

the species which form the connections between lichens and other fungi will be at all satisfactory.

The lichen may be defined thus: *A lichen is a fungus which lives during all or part of its life in parasitic relation with an algal host and also sustains a relation with an organic or an inorganic substratum.* It need scarcely be pointed out that this definition is a biological rather than a morphological one, and that we are treating lichens from a biological rather than a morphological or a taxonomic point of view. Our definition denies the mutualism hypotheses, to one of which some of us have adhered for many years; nor does it meet very well the requirements of those who hold that the group Lichenes should be retained. Of course, the lichen is usually parasitic on many individuals of some species of alga, instead of living on a single individual. One may speak of the alga or the algal host, meaning the species on which the lichen is parasitic, or one may, with equal propriety, speak of the algae or the algal hosts on which the lichen is parasitic, meaning thereby the individuals. The definition above follows the first method. Likewise, as pointed out by Bonnier (31), Friederich (59), Stahlecker (125) and Zukal (149), what is called a lichen individual is often compound, being composed of a number of simple individuals united. Our definition defines the simple individual. Again, the lichen is probably partly saprophytic on the alga. It does not seem necessary to recognize this point in a definition of the lichen, for the present at least. One or two of Zukal's half-lichens are not known to sustain the relationship with the external substratum and if they do not, may be excluded from lichens on this account.

THE ALGAL HOSTS OF LICHENS

For some of us, it would not be necessary to consider the nature of lichens further; but for those who still cling to the dual hypothesis, the last word will not be said until the relation of the lichen to its algal host has been thoroughly reviewed. A considerable number of algae have been enumerated as lichen hosts, but most of these rarely or never function as hosts for lichens. Fünfstück (64) gives ten algae known as lichen hosts. These are *Chlorococcum* (*Cystococcus*) *humicola, Palmella botryoides,*

Trentepohlia (*Chroolepus*) *umbrina, Pleurococcus vulgaris, Dactylococcus infusionum, Nostoc lichenoides*(?), *Rivularia nitida, Polycoccus punctiformis, Gloeocapsa polydermatica* and *Sirosiphon pulvinatus.* Of these the larger number are blue-green algae, yet the two species of green algae, *Chlorococcum humicola* and *Trentepohlia umbrina,* form the hosts of many more lichens than all the others combined. So far as the writer knows, *Palmella botryoides* is the host of only one little-known lichen, viz., *Epigloea bactrospora* Zuk.; and there is better reason for including among lichen hosts one or more *Scytonemas* which are algal hosts of the better known *Dictyonemas,* also of one of Zukal's half-lichens, and may sometimes be the host of *Stereocaulons* as well. Only a few lichens are known to live facultatively on different algae, most lichens being obligative parasites. *Lecanora granatina* Sommerf., *Solorina crocea* (L.) Ach., the *Cypheliums, Pannaria tryptophylla* (Ach.) Mass. and probably a few others are facultative. The facultative species are either those which have never settled upon a definite host, or those which are changing from one host to another. But such change is probably rare and so slow a process as scarcely to come within the range of observation.

Lichens usually parasitize terrestrial algae which grow in habitats commonly invaded by lichens. This accounts for the small number of algal hosts of lichens. It is well known, as will be brought out below, that lichens frequently attack free algae and that parasitizing algal individuals or colonies, of species which have long formed lichen hosts, is going on constantly. On account of the modification of the algal hosts, due to parasitism, there is still some uncertainty regarding certain species of algae that serve as lichen hosts; and it would not be strange if the number of closely related species that function as such hosts is larger than we now suppose. Lichens are known to parasitize approximately one per cent. of known species of blue-green algae and a very much smaller proportion of the numerous green algae.

FINDING THE ALGAL HOSTS GROWING NEAR LICHENS

Schneider (111) thinks that the spores of lichens are degenerate and do not often function for reproduction. We often find algae which, under the microscope, show plainly the presence of

attached fungal hyphae, but Schneider thinks that these are not the primordia of any well-known higher lichens. Hicks (67) found that if a piece of bark supporting *Chlorococcum* is kept under glass in a moist place, the groups of algal cells seem to become transformed into a felted mass. We now know that the same thing is often observed in nature, lighter felted masses often appearing where *Chlorococcum* has been growing. Microscopic examination shows that the color change is due to the development of lichen hyphae. These hyphae appear more commonly when the alga grows near some lichen, and it may take years for the felted, mycelial masses to develop into mature lichen thalli.

We have observed, in our laboratory with our students, minute *Nostoc* colonies, germinating *Collema* spores, other *Nostoc* colonies penetrated by one or more germ tubes of spores, and various stages of development of *Collemas,* all growing together. When first parasitized by the lichen, the *Nostoc* colonies are of normal form; but as the lichen develops within, the algal colonies become greatly modified in form. The *Nostoc* colonies are usually parasitized when only 50 to 200 mic. in diameter.

Likewise, Schwendener (119) records finding free *Nostoc* colonies, others penetrated by several *Collema*-like hyphae, young but undoubted *Collemas* on scarcely modified *Nostoc* colonies, and older *Collemas* on much modified *Nostoc* colonies, all growing together in the field. He also found similar relations between *Leptogium subtile* (Schrad.) Koerb. and *Nostoc* colonies, between a species of *Placynthium* (*Racoblenna*) and *Rivularia,* between *Ephebe pubescens* (L.) Fr. and *Sirosiphon,* and between *Spilonema paradoxum* Bor. and the same alga. Kny (72) recorded finding *Lichina pygmaea* Ag. and its algal host, *Rivularia nitida,* growing in proximity in the same clusters, in some portions of which the *Rivularia* individuals were all free, in others all parasitized by the lichen, and in still other portions, partly free and partly parasitized.

Bornet (33) found *Trentepohlia umbrina* forming the algal host of *Opegrapha varia* Pers. and also growing on the branches of trees about the lichen, but separate from it, both on the outer surface and within the periderm. Toward the margin of the

thallus of this *Opegrapha*, he noticed loosely felted hyphae within the periderm and upon the surface, the hyphae becoming scarce at the margin. Where these hyphae encounter free *Trentepohlia* filaments, they become attached to the algal cells. He found the same relationship between *Trentepohlia* and *Pyrenula nitida* (Weig.) Ach. and also recorded finding the *Trentepohlia* filaments from within the lichen thallus extending into external filaments, which produced zoöspores while still attached to the lichen. He also found that the same alga produces zoöspores within the thallus of *Opegrapha varia* Pers., and that the lichen hyphae are often attached to zoösporangia of the algal host. The same worker found the algal host of *Pannaria nigra* (Huds.) Nyl. extending into external filaments, which sometimes become free from the lichen. Like de Bary, he found *Nostoc* parasitized by *Collema*, but showing minute tubercles, often nearly cut off from the lichen. Some of these tubercles become free and form minute, non-parasitized *Nostoc* colonies, at first not over a half millimeter in diameter. Zukal found *Palmella botryoides*, both free and parasitized by the lichen, *Epigloea bactrospora* Zuk.

Cunninghan (43) and Ward (138) both studied the relationship of *Strigula* to its algal host and to the leaves on which the lichen and its algal host grow together. Cunningham found that the lichen produces fruit only after parasitizing the alga, and that the alga forms zoöspores, oögones and antherids only when free from the lichen. Ward found the leaves of *Michelia fuscata*, especially during the rainy season, to contain networks of branching mycelia of *Strigula complanata* (Fée) Nyl. These mycelia are composed of brown, septate, branching hyphae, spread over the leaf-surface without haustorial attachment. They rise from oval, brown, two-celled ascospores, and often produce clusters of brown conidia. A *Trentepohlia*-like alga also grows here and there on the leaves, and the algal groups are often overgrown by these mycelia, which produce the conidia where they come in contact with the algae. The hyphae gradually penetrate into the algal masses, destroy them, and in the meantime produce spermagones and later perithecia. The lichen sometimes parasitizes the alga while the latter is very young, and the algal host is soon

killed, the lichen producing conidia but neither spermagonia nor ascospores. But when the attack comes later, it takes longer to kill the alga, and the lichen produces spermatia and ascospores. Finally, some of the algae run their whole life history without being attacked by the lichen.

Nylander (97) held that he found lichens most abundant where algae are absent; but he doubtless based his statement on an erroneous impression and not on careful observation. Peirce (98) finds commonly on old fences free algal cells, others invested by hyphae and so on up to mature lichens of various species common in his region. Williams (141) observed that lichens appear first in damp places, where algae are most numerous, and spread gradually from these to other locations. He found that they grow first on the shady and moist parts of trees and fences and rarely if ever appear first on dry, wind-exposed portions. These observations of Peirce and Williams agree in general with what the writer has noted many times, though there is no doubt that lichens will grow in very dry places.

We have many times found the algal clusters which proved to be parasitized by fungal hyphae, growing both in the vicinity of lichens and in other moist places, but have not been disposed to agree with Schneider that these are necessarily the primordia of very primitive lichens. It has seemed more reasonable to suppose that they may be young conditions of higher as well as of lower lichens which are present in mature form near by. Years of observation of the development of these primordia should give valuable results, whether growing in the vicinity of lichens or elsewhere.

Nylander (94) mentioned algae occurring in the hymenia of pyrenomycetous lichens. Fuisting (62) found that in *Stigmatomma cataleptum* (Ach.) Koerb. the hymenial algae are certain algal host cells, which become imprisoned in primordia of apothecia and multiply as the apothecium develops. Winter (143) agreed in general with Nylander and Fuisting, all three finding that the hymenial algae are smaller than other algal host cells; but Winter noted in addition the paler color of the former. These hymenial algae occur in early stages of development, or in

old apothecia of many lichens; but they seem to be especially characteristic of pyrenomycetous lichens, particularly those that have muriform spores. Stahl (124) found them in *Endocarpon pusillum* Hedw. and in *Polyblastia rugulosa* Mass. and proved that, in these lichens, they are ejected with the spores, which soon germinate and attack the algae. Little is really known about the frequency of occurrence of hymenial algae at the time that spores are ejected; but it is probable that this is not uncommon in those pyrenomycetous lichens which are not able to live a considerable length of time outside the parasitic relationship with an algal host. Hymenial algae perform somewhat the same rôle as the algae in the soredia of higher lichens; and since they occur in lower lichens, while the soredia are more common in higher lichens, each of these provisions for reproduction supplements the other. Even in lichens that have neither soredia nor hymenial algae, there is no difficulty about reproduction through lichen hyphae coming in contact with algal host cells. Since spores blow long distances, this could happen whether lichens grow near the algal hosts or not.

These various observations regarding lichens growing in proximity with their algal hosts prove that lichens may frequently originate from spores which germinate and attack free algae; and it must be borne in mind that the spores may remain dormant for a considerable length of time until conditions favorable for germination are at hand. Such observations also show that both the algae and the lichens may grow separate from each other, the former throughout their whole life and the latter sometimes during a considerable time, very probably years in some instances. Such results make the consortium hypothesis wholly invalid, and seem to have been overlooked, underestimated or misinterpreted by those who hold to that hypothesis.

Cultures of Lichens With or Without the Algal Hosts

Alfred Möller (87) cultivated *Lecanora subfusca* (L.) Ach., *Thelotrema lepadinum* Ach., *Pertusaria communis* Lam. and DC., *Graphis scripta* (L.) Ach., *Buellia punctiformis* (Nyl.) Hoffm., *Lecidea enteroleuca* Ach., *Opegrapha subsiderella* Nyl., *Arthonia*

vulgaris Schaer., *Calicium parietinum* Ach., *Calicium trachelinum* Ach., *Calicium curtum* Borr. and Turn. and *Verrucaria muralis* Ach. from spores, from spermatia, or from both spores and spermatia, without the algal hosts. The following five, *Buellia punctiformis* (Nyl.) Hoffm., *Opegrapha subsiderella* Nyl., *Calicium parietinum* Ach., *Calicium trachelinum* Ach. and *Calicium curtum* Borr. and Turn. were cultivated from both spores and spermatia. With *Graphis scripta* (L.) Ach., he obtained hyphal tangles which he regarded primordia of apothecia, or of spermagonia; but the purpose of his work was not to determine whether apothecia can be produced when the lichen is grown without the algal host, and some of these crustose lichens might have fruited, had the cultures run more than a few months. Again, he might probably have obtained apothecia, had he worked on *Endocarpon pusillum* Hedw. or *Polyblastia rugulosa* Mass., which are known to mature and to produce apothecia from the spores in two or three months. He tells very convincingly of obtaining spermagones in cultures of *Calicium parietinum* Ach. in five or six weeks, from spores and from spermatia. Beginning with spermatia produced in pure cultures, he obtained several successive generations of thalli by the germination of these bodies, and thus proved that the ascopores and the spermatia belong to the same plant. He also obtained spermatia in nearly all of the cultures and got them to germinate and produce new thalli of the same kind as those on which they were produced. His results indicate that these structures are either asexual conidia or male cells which have the power of reproducing parthenogenetically. In further studies Möller (88) obtained branched germ tubes from the spermatia of *Collema microphyllum* Ach.

Möller is not the only one who has caused spermatia of lichens to germinate, but we must now pass to some observations by Hedlund (66). He found spermatia of *Catillaria denigrata* (Fr.) Hedl. and *C. prasina* (Fr.) Th. Fr. which had germinated on the natural substratum among mature and variously developed states of these lichens and the free algal hosts. The mycelium produced by the spermatia was growing alone in some instances, while in others it had parasitized some of the algae. The latter lichen

showed many intermediate conditions between the young mycelia produced from the germinating spermatia and the mature plants with spermagonia and apothecia. The spermatia germinating on the substratum were compared with those found in the spermagonia and were like these and also like those germinating on the thalli about the spermagonia. These results confirm those of Möller and are also interesting because they give further evidence of lichens growing with the algal hosts and reproducing by germinating upon them.

Bornet's classic results (32) are well known. He grew lichens from spores and found that they readily attack their algal hosts, while those that do not come in contact with the algae soon die. Of course he did not use proper media, or his lichens might have grown longer without the hosts; but this failure matters not for our purpose. He grew species of *Collema, Arnoldia* and *Physma chalazanum* (Ach.) Arn. with *Nostoc* colonies, *Synalissa* and *Omphalaria* with *Gloeocapsa, Ephebe* with *Sirosiphon, Opegrapha varia* Pers., *Roccella phycopsis* Ach. and *Pyrenula nitida* (Weig.) Ach. with *Trentepohlia, Opegrapha filicina* Mont. with the *Coleochaete*-like *Phyllactidium* and a number of lichens with *Chlorococcum humicola.* He found *Pannaria tryptophylla* (Ach.) Mass. to grow with two algal hosts, a *Nostoc* and a *Scytonema.* Both of these algae often occur with the lichen in nature, and both often are found in the same lichen thallus. He also found *Trentepohlia* and *Phyllactidium* free in the vicinity where *Roccella, Opegrapha* and *Verrucaria* were growing. *Opegrapha filicina* Mont. is an ectoparasite, and some other lichens are also ectoparasites, but on unicellular or filamentous algae, among which the hyphae grow without penetrating into them. For instance, there is no connection between the *Collema* hyphae and the *Nostoc* filaments; and the *Collema* is ectoparasitic, except for penetrating into the gelatinous envelopes of the *Nostoc* colonies. The *Nostoc* individuals are nearly normal, but the colonies are much modified in form. Bornet also found *Pannaria muscorum* (Ach.) Del., *Lichina confinis* (Smith) Ag. and *Heppia urceolata* Näg. parasitic on two algal hosts, the last two with *Chlorococcum humicola* and a blue-green alga. He found that the other lichens

studied attack the cells of the algal hosts directly; and in such instances the algal cells or filaments are so modified or broken up that the nature of the algal host is difficult or impossible to ascertain. But where the union of hyphae with algal-host cells can not be seen, the latter are little, if at all, modified. In this connection, it may be added that Bornet saw his algae growing in the usual form and also modified by the lichen parasites, and so established that the modification is not phylogenetic but comes about rapidly. He referred his algal hosts to the genera *Trentepohlia, Phyllactidium, Chlorococcum, Pleurococcus, Dactylococcus, Ulothrix*(?), *Cladothrix*(?), *Scytonema, Nostoc* and *Oscillatoria*. These are nearly all cosmopolitan algae, to be expected on barks, earth, bases of mosses and in cracks and crevices where lichens may begin development from spores and attack their algal hosts.

Treub (135) caused lichen spores to germinate in pure cultures in the hope that he might develop the green cells from the hyphae. Of course he failed in this. Then he made cultures from spores of *Xanthoria parietina* (L.) Th. Fr., *Ramalina calicaris* (L.) Fr., *Lecanora subfusca* (L.) Ach. and *Physcia pulverulenta* (Schreb.) Nyl., with the algae present and found that the germ tubes of the spores lay hold on the algae. He used wild *Chlorococcum humicola* and obtained the same results as when he took the algae from lichen thalli. He thus proved that the germinating spores may readily attack free algae, as would be inferred from the fact that lichens so frequently grow in the vicinity of the free algae. He got the hyphae to branch freely after attacking the algae, but did not get fully developed thalli. Borzi (34) made cultures of *Physcia pulverulenta* (Schreb.) Nyl., *Physcia ciliaris* (L.) Ach., *Xanthoria parietina* (L.) Th. Fr. and *Pertusaria communis* Lam. & DC. with algae, and concluded that these lichens are Ascomycetous fungi and are parasitic on the algae with which they grow.

As briefly outlined above, Möller (89) found a small white thelephore growing with the lichen, *Cora*. The fungus rarely occurs elsewhere than on the same substratum and in the same locality with this lichen. The general structure is the same in both plants, and their spores behave alike in germination. He

pulverized portions of the lichen in water and poured the broth over thelephore plants. In three months there appeared on lobes of the non-algicolous plants thus treated, and only on these, typical algicolous *Cora* lobes. By microscopic examination, he found that the pulverized lichen tissues did not grow; but rather that the thelephore hyphae attacked the algae and became transformed into *Cora* lobes, which appeared only at the margin of the thelephore, where its hyphae came in contact with the algae. In some instances the algae were left behind in time, and the *Cora* lobes reverted into thelephore forms. Thus he effected in nature the transformation of a non-algicolous into an algicolous fungus (lichen), and vice versa. Microscopic study proves that the spores of *Dictyonema, Laudatea* and *Cora* are alike, and behave exactly alike in artificial cultures. The thelephore which passes into the *Cora* form when it parasitizes *Chroococcus* grows into *Dictyonema* or *Laudatea,* according to conditions of habitat, when it parasitizes *Scytonema, Dictyonema* being confined to small branches not more than finger-thick, and *Laudatea* occurring on larger branches, on dead wood, on leaves, on mosses, or on liverworts. Transitional forms between *Dictyonema* and *Laudatea* occur commonly. *Cora* forms grow from *Dictyonema* lobes, and the thelephore is found growing from *Cora* lobes and from *Dictyonema* lobes. *Laudatea* grows on *Dictyonema* lobes, or on *Cora* lobes, in response to change in algal host. Fungus individuals growing on the spherical cells of *Chroococcus* would be modified less and in a different manner from those growing on *Scytonema* filaments, and so *Cora* is more like the thelephore than are *Laudatea* and *Dictyonema,* which are more modified on account of the nature of the algal host. We may still regard the genera *Cora, Dictyonema* and *Laudatea* distinct from each other and from their thelephoric progenitor, though any one of these may be produced from any other one in a short time by absence or by modification of the relation with an algal host. Yet this taxonomic distinction can not be insisted on very strongly. Möller's research shows plainly that it would be absurd to regard such lichens anything but fungi. Nor do other lichens behave so differently toward their algal hosts as many botanists have supposed.

Bonnier (31) seems to have been first to produce mature, fruited lichens in cultures. He raised *Xanthoria parietina* (L.) Th. Fr. with an alga which he called *Protococcus* and succeeded in getting a thallus that bore an apothecium. With the same alga, he obtained fully developed thalli of *Physcia stellaris* (L.) Nyl. and *Parmelia acetabulum* (Neck.) Dub., but he got no apothecia in these. He sowed *Rinodina sophodes* (Ach.) Koerb. with *Pleurococcus* and got well-developed thalli with apothecia. *Lecanora ferruginea* (Huds.) Nyl., *Lecanora subfusca* (L.) Ach., *Lecanora coilocarpa* (Ach.) Nyl. and *Lecanora caesiorufa* (Ach.) Nyl. grew to maturity with the same alga in two to four years, but none of these produced fruits. Unless he was mistaken in his alga, the algal host was not only wild but also unusual; but he might easily have mistaken *Chlorococcum* for *Pleurococcus*. Spores of *Opegrapha vulgata* Ach. sown with *Trentepohlia* produced good thalli as did also *Verrucaria muralis* Ach., in less than a year. He got *Lecanora atrorufa* Ach. spores to germinate on *Trentepohlia* and *Lecanora subfusca* (L.) Ach. spores on *Vaucheria sessilis*. The former showed haustoria and a poor development of plectenchyma, but the latter produced the plectenchyma only. All of these were cultures with wild algae, and prove that these algae are quickly modified, when parasitized, into the forms usually found in lichens.

Tobler (130) cultivated *Xanthoria parietina* (L.) Th. Fr. with and without an alga. He found that when the lichen grew alone, the yellow parietin was not developed; and treatment with acids and alkalis did not produce the characteristic coloration. In cultures of the same age with the alga, he got the yellow parietin and the characteristic chemical reactions. Zopf (148) has summarized these peculiar chemical reactions and the colors produced in lichens, and Tobler's results indicate that all of these chemical reactions and colorations are due to the peculiar relation of the lichen to the algal host, the former plant not being able to produce them alone. So the lichen differs from other fungi in the production of peculiar substances when it grows with the host.

The greatest advantage of parasitism on the algal host has been supposed to be that the lichen received carbon, which the alga

obtained from the air. But now, through another work of Tobler's (132), reinforced by some other researches, it appears reasonable to suppose that the lichen may furnish the alga a portion of the carbohydrates which the former receives from the substratum. Tobler cultivated *Xanthoria parietina* (L.) Th. Fr. and some other lichens without algae in a beerwort-gelatine medium and got a rich production of calcium oxalate. He then grew the thalli with the algae and was not able to find the oxalate. Therefore, he supposes that the algae use the surplus extracted from the medium by the lichen, and that the same thing may occur in nature, the lichen taking the oxalate from the organic substratum. Tobler also started *Xanthoria* on gelatine and transferred it to a liquid medium which contained none of the carbon compounds needed by the alga, except what was contained in the air, and the lichen grew somewhat. The alga increased in the same liquid medium and was of normal appearance. In transferring the lichen, particles of the gelatine were unavoidably carried over. After these were probably consumed by the lichen, the alga was introduced into the culture with the lichen and grew well, but was colorless. This he thinks indicates that the lichen had assimilated the acid, probably oxalic, which the alga needed as a source of carbon. He says that gelatine is not a source of carbon for the alga, so that his conclusions would not be invalidated even if the lichen had not extracted all of this substance from the medium before the alga was introduced. The lichen hyphae soon entwine some of the algal cells in the culture, and thus the parasitic relationship is established. Tobler believes that the lichen obtains carbon from the alga, while the latter replaces it by extracting carbon from the oxalic acid contained in the tissues of the lichen. This would mean an exchange of food particles between the lichen and its algal host in the cultures. While this may be true in his cultures, it could scarcely be so in instances where the lichen grows on rocks that contain no organic matter. But organic substances accumulate very soon, on or in all exposed rocks; so all rocks on which lichens grow may have sufficient organic matter. However, there is no certainty, if indeed any probability, that the physiological relation of the lichen

to its algal host is, in nature, like what occurs in cultures. It is more probable, after all, that the lichen simply carries from the substratum whatever food it gives to the algal host. Yet the lichen may assimilate, or at least digest, some of this food before it is used by the algal host. Tobler obtained the same results with *Pertusaria communis* Lam. & DC. and *Parmelia acetabulum* (Neck.) Dub. So the conclusion is that the lichen produces the oxalate in the cultures, and that the lichen consumes it in each instance. Multiplying instances of such action in cultures can not give us certain knowledge of what happens in nature.

The only certain thing shown by these experiments is that the lichen stores up substances when growing alone in cultures, which are not stored when it grows with the alga, since this host plant uses these substances as a source of carbon. In *Pertusaria* and *Diploschistes,* Tobler found oxalic acid cystals present in thalli which contained algal host cells. He supposes that, in these and other lichens that have thin cortices, the algal host secures sufficient carbon from the air and does not utilize that secured by the lichen from the substratum. In lichens that have thick cortices, the alga would have greater difficulty in securing carbon from the air and would be more likely to depend in part, or perhaps wholly, on materials taken from the substratum by the lichen.

THE GROWTH OF LICHEN HOSTS AND OTHER ALGAE IN PURE CULTURES

Treboux (133) found that species of *Chlorella, Pleurococcus, Cystococcus* and some other algae are able to obtain carbon in a very different manner from that known in higher green plants. These algae are able to thrive on artificial media containing organic acids, and so he reached the conclusion that they behave like fungi with respect to carbon assimilation. Artari (7) grew *Chlorococcum humicola,* obtained from the thalli of *Xanthoria parietina* (L.) Th. Fr. and *Placodium murorum* (Hoffm.) Ach., in pure cultures on complicated media containing mineral salts or organic compounds, or in some instances, both the mineral salts and the organic compounds. He found that the alga grows and multiplies luxuriantly on the media containing organic matter and is dark green in color, though grown in absolute darkness or in light with

CO_2 excluded. On media containing mineral salts but no organic matter, the alga grows, but not so well. These results square beautifully with those of Tobler on one of the same plants, one worker giving special attention to the lichen and the other confining himself to the algal host. The two researches prove that the alga which lives in the thallus of *Xanthoria parietina* (L.) Th. Fr. can obtain its organic matter and its mineral salts from the lichen. Radais (110) cultivated *Pleurococcus vulgaris* in total darkness on media containing albuminoids or hydrocarbons and found that it can utilize these substances as do saprophytic fungi and bacteria, and that it grows as rapidly and produces chlorophyll as well as in its ordinary habitat. The chlorophyll was analyzed with the spectrum and was found to be normal. So far as they go, these results confirm those of Treboux and Artari. Beijerinck (19), Bouilhac (51), Etard (51), Klebs (71) and others have also obtained results with algae in pure cultures, somewhat similar to those of Treboux and Artari. Two of these workers studied blue-green algae, which behave in the same manner as the green algae.

Beijerinck (19) cultivated the algal host of *Physcia* in elm-bark gelatine, with malt extract added. This alga, *Cystococcus* according to his results, he thinks, is not common in his region, except as the host of lichens, but is replaced in free nature by *Pleurococcus*. The *Cystococcus* was found to have no vacuole or pyrenoid, though other authors seem to find both vacuoles and pyrenoids in algae growing in lichens. The alga produced zoospores in pure cultures, freed from the lichen. His results are valuable, but it is very doubtful whether he found an algal host of lichens which is not common in the free state in the same region. Baranetsky (14) cultivated thin sections of *Collema pulposum* (Berhn.) Ach. and the portion of the algal colony contained. He got young *Nostoc* colonies, which grew rapidly, while the lichen died. He obtained similar results with *Peltigera canina* (L.) Hoffm. Famintzin and Baranetsky (54) isolated algae from the lichen parasites, and the algae produced 30 to 60 zoospores after the manner of free *Chlorococcum humicola*. They worked also on the hosts of *Xanthoria parietina* (L.) Th. Fr., *Evernia fur-*

furacea (L.) Mann and *Cladonia* sp. with similar results. Finally, they found the same algae growing free with lichens in their natural habitats and secured zoospores in similar manner from these.

Itzigsohn (69) made cultures for the purpose of ascertaining the systematic position of *Peltigera*. He found that the algae could be cultivated independently, and that they are blue-green, 20 or more cells often cohering in the cultures in chain-like form, resembling *Anabena*, while in other instances the cells are arranged in colonies resembling *Chroococcus*. Woronine (144) isolated the algae from *Physcia pulverulenta* (Schreb.) Nyl. and obtained 30 to 40 zoospores from each individual in the cultures.

It will be noted that the last section also gives something concerning cultivation of the algae separately, the two kinds of cultures often going on in such a manner that the results are best given together. Those who hold to the mutualism hypothesis have claimed that the algal hosts of lichens are more difficult to cultivate than the same species of algae when free, but there is nothing to indicate that this is true.

THE GROWTH OF LICHEN HOSTS AND OTHER ALGAE ON MEDIA WITH LIGHT OR CARBON DIOXIDE EXCLUDED

Reference was made to this matter in the last section above, in an incidental manner. Treboux (133) found organic acids to be the source of carbon for a number of algae in cultures in total darkness. Some of the 40 algae used are *Stigeoclonium tenue, Scenedesmus obtusus, Raphidium polymorphum, Stichococcus bacillaris, Pleurococcus vulgaris, Chlorella viridis, Chlorococcum humicola, Haematococcus pluvialis, Euglena viridis* and the algal hosts of *Peltigera* sp. and *Xanthoria parietina* (L.) Th. Fr. Of the 40 algae, about half were found to assimilate from media containing organic acids, some growing better with one acid, others with another. He concluded that there is no such sharp distinction between fungi and algae with respect to carbon assimilation as had been supposed, the former probably being able to extract carbon from a larger number of organic compounds than the latter. Then the method of assimilation for the lichen and its algal host may not be so different after all. Whether terrestrial

algae take much carbon from the substratum, except in cultures, may well be doubted. It is scarcely likely that they live a purely saprophytic life in nature as they may be made to do in artificial cultures. It is, on the other hand, much more reasonable to suppose that algae confined in lichen thalli accomplish part of their carbon assimilation saprophytically in the absence of abundant light and air. Lindau (81) noted that *Trentepohlia* seems to flourish better in darkness of deep layers of bark than in the better lighted portions; and it is reasonable to suppose that those algae which live in the bark of trees are nourished somewhat like fungi, whether serving as algal hosts for lichens or not.

As stated above, Artari (5) found that the algal hosts of *Xanthoria parietina* (L.) Th. Fr. and *Placodium murorum* (Hoffm.) Ach. grew on peptone and sugar containing media in absolute darkness and in light with CO_2 excluded, and remained dark green for the time that the cultures were run,—about one half to two and one half months. These algae grow well on mineral salts under the same conditions, but not so luxuriantly, and are usually pale green on these salts. In such cultures, the peptone doubtless serves for nitrogen and the sugars for carbon. Artari tried several modifications of media with varying results. This confirms again the view that the algal hosts of lichens are not very dependent upon light or air. Yet it is doubtless true that the algae in lichen thalli work at a disadvantage on account of scarcity of light and air, and could perform carbon assimilation better with both of these present in larger quantity, such forms as *Trentepohlia* being excepted perhaps. Artari (6) carried on similar experiments with *Stichococcus bacillaris,* the algal host for certain lichens, with results like those stated above.

Regarding the general relation of lower algae to carbon assimilation, Artari's final conclusion (7) is more extreme than might be expected. He thinks that these plants are more dependent upon the nature of the substratum for chlorophyll production than upon either light or CO_2. He found that certain lower algae remain colorless on certain media with light and CO_2 admitted, but are deep green on other media with light and CO_2 absent. This rather independent relation of such plants to light and CO_2

adds to the ease with which some terrestrial algae may have assumed the hostal relation with lichens. It shows that these algae need not have undergone any great change in method of nutrition since becoming lichen hosts. Again, according to this, certain algae may at any time become hosts of lichens without any pronounced nutritional change, the modification being almost entirely morphological and physiological, due to the effect of the lichen upon form, size and functioning of the algal cells or filaments.

It is plain enough that these results from physiological researches are in part conflicting, and that more investigation is needed.

BREATHING PORES AND OTHER MEANS OF AERATION FOR LICHENS AND THEIR HOSTS

Breathing pores have been postulated for lichens, and their existence in crude form in some lichens is no longer to be doubted. Yet their general presence is not proved. Fünfstück (64) gives a general summary in Engler and Prantl. Rosendahl (107) says that *Parmelia aspidota* (Ach.) shows numerous wart-like elevations. These are at first small and closed above; but they enlarge and open later, so that there is free communication between the interior of the thallus and the external air. The openings are formed by a loosening of the hyphal tissue of the plectenchymatous cortex, so that they are not definite canals, but passages through networks of hyphae. He found no such system in any other of fourteen species studied from the same genus and concluded that its presence in *Parmelia aspidota* (Ach.) is correlated with the unusually thick cortex of this species. Zopf (147) has described a new species of *Ramalina* which has similar structures. Aside from such passages which are known in very few lichens, there are several possible ways of entrance. Air may enter through growing points, where the cortex is only one or two layers of loosely interwoven hyphae, and through the lower sides of thalli that have no lower cortices or very thin or incomplete ones. In thalli with uneven upper surfaces, the cortex is often very thin over the elevations, where air may enter. Other

thalli have cracks, through which air may readily reach the medulla. Soralia, cyphellae and empty spermagones furnish avenues, through which air may enter. Isidioid branchlets have thin cortices at their summits, through which air may gain entrance. Hollow cylinders in the center of certain fruticose thalli serve as air chambers, and these are sometimes in direct communication with the exterior through dying away of the basal portions of the branch.

The most extended studies are those of Zukal (153). This worker thought that the hyphae of the medulla of lichens, on account of their branching and elasticity, might be well adapted for retaining air in the interior of the thallus, and for giving it up to the tissues of the lichen and the algal host as needed. The cortex of many lichens becomes pure white after the surface has been moistened, the coloration being due to the air retained within the plectenchyma. When the cortex is brought into water under cover glass on a slide, treatment with alcohol is necessary to drive out the air, the numerous air bubbles disappearing rather slowly. Since the plectenchyma of the cortex admits air with great difficulty, Zukal supposed that the hyphae of the medulla must pass the air admitted to the interior of the thallus upward to the algal host cells. The difficulty with this is that it makes aeration dependent upon such crude makeshifts for getting the air into the interior of the thalli as have been enumerated above, and these do not seem sufficient for adequate exchange of gases for the algal hosts.

Zukal found that when he placed a crustose lichen in glycerine or clove oil and observed with high power hand lens, he saw black, glistening air bubbles under the liquid at numerous points where the atmosphere seemed to be in easy communication with the medulla. This he was able to demonstrate for hypophloeodal and for hypolithic crustose lichens as well as for those above the substratum. He also found that if thin sections through the thallus of a lichen that is parasitic on a gelatinous alga be dried and brought into water-free glycerine, a large number of black, air-containing lines and dots appear in the transparent mass. These black lines and dots pierce through the sheaths of the gelatinous *Nostoc* or *Gloeocapsa* colonies and often follow the

lichen hyphae and the trichogynes. His observations with dry sections in glycerine were also extended to many foliose and fruticose lichens with similar results; and he concluded that the thalli of lichens are richly provided with means for aeration.

It will be noticed that all of the means for aeration enumerated above are not real canals but loose passages between entangled hyphae, and that most of them are accidental or occasional. We have taken pains to confirm Zukal's observations upon the air content of dry sections in glycerine and find the air bubbles in lines and spots. The glycerine treatment then proves the presence of air in lichen thalli. The occurrence of thin places in cortices, the soralia, the cyphellae, the empty spermagones, the hollow cylinders, the crude canals and other makeshifts are a matter of common knowledge among students of lichen anatomy. But after all this is admitted, we are still not convinced that sufficiently rapid air movements and the means for sufficient aeration of the algal hosts in lichens are present. These hosts have greater need for aeration than the lichen itself, which needs air only for respiration, while the alga could use it also for carbon assimilation. Furthermore, the air enters through openings in the tissues of the lichen, which is reached directly, while many of the algal host cells are reached only by a slow circuitous route downward or upward through the cortex, thence through or along the hyphae of the medulla. We are of the opinion that nothing but definite air canals, leading directly from the exterior to all the algal groups within the lichen, could accomplish aeration for these algal cells in an efficient manner.

Schneider's results (111), obtained during the time that Zukal was working, add little to those of the latter worker. Schneider observed algae extending almost to the upper surface, in circumscribed areas, in lichen thalli which had thick cortices elsewhere than in these areas. He also saw, in certain lichen thalli, intracellular spaces passing from some of the algal clusters through the cortex and the epidermis to the exterior, taking a circuitous instead of a direct route, and often following almost a horizontal course in the epidermal layer. He found these crude canals closed when the thalli were dry. His statements read quite as convincingly as those of Zukal, but we can not accept the results

as accounting for sufficient aeration of the algal host within the lichen thallus.

Jumelle (70) worked from the physiological point of view instead of the anatomical. His results show that there is an exchange of gases to and from the exterior for lichen thalli and for the algal hosts, both in light and darkness and at low and high temperatures. But he failed to differentiate between the work of the lichen and its host, and his results seem more uncertain than those of Zukal and Schneider, who worked from the anatomical point of view. Jumelle thought that, instead of the thallus taking part in the process as a whole, there must be special contrivances for aeration. But he did not attempt to prove this, and the results of others seem insufficient.

According to more recent ideas of parasitism of the lichen upon the alga and the ability of the latter to receive nourishment from organic compounds brought up from the substratum by the former, the alga can get along without special provision for its aeration, but would doubtless thrive better were aeration abundant. In fact, it does not appear that lichen evolution has made any special provision for aeration of the algal host as would be required by the mutualism hypothesis. It seems rather that the lichen has developed in a manner best adapted to its own advantage, and that the alga suffers more or less from lack of sufficient aeration, unless it chances to be a species that can secure carbon from the substratum through the lichen quite as well as from the air.

THE RELATION OF THE LICHEN TO ITS ALGAL HOST

Some algal hosts, as *Nostoc, Sirosiphon, Trentepohlia, Scytonema* and *Phyllactidium,* are in contact with the substratum, from which they take food directly; but the conditions of parasitism of most lichens upon the algae are such that the algal hosts become completely surrounded by the parasitic lichen and raised from the substratum. It is this peculiar condition of parasitism, in which the unicellular or the filamentous host is surrounded by the parasite, instead of the parasite being surrounded by the host, or covering only a portion of its surface, as we find in the more usual conditions of parasitism, that has led to the erroneous views re-

garding the relation of the lichen parasite to its algal host. Thus it comes about that many botanists have thought the relation to be mutualistic, some even going so far as to suppose that the host and the parasite together constitute an individual, working in harmony much like the parts of an ordinary automaton. But the facts do not favor this supposition. The host is placed in a disadvantageous position regarding food supply, and then more or less of its food is probably carried to it from the substratum with which it would be in direct contact, were it not for being parasitized by the lichen, which imprisons it and removes it from the substratum. We see nothing in this, on the whole, but disadvantage to the algal host, which could secure its food more easily, were it not parasitized.

Arnoldia and *Physma* are the only lichen genera parasitic on *Nostoc,* which send haustoria into the cells of this algal host, or even come into close enough relation with these cells to effect any change in their form or that of the filaments which they compose. Otherwise, the cells or the filaments of the algal hosts of lichens are more or less modified by the parasitism. Yet one may find, commonly enough, algal cells or filaments not yet parasitized, which show the normal form for the species. In the case of *Nostoc,* where the cells are not usually affected, the whole colony is nevertheless modified in form by the parasitic lichen, as is illustrated by species of the Collemaceae.

Bonnier (31) germinated spores of *Physcia apiolia* (Ach.) Nyl. on the protonemata of mosses and found that the hyphae invest the protonemata, form a plectenchyma and haustoria and sap the protonemata of nourishment. Those on which the lichens grow are smaller than those not parasitized, and are often killed outright, though the haustoria do not penetrate into the cells of the protonemata. He found also that the same often occurs in *Cladonia pyxidata* (L.) Hoffm., when the spores germinate on protonemata and grow as above explained. Sometimes algae fall upon the lichen growing on the protonemata, when the algae become parasitized, and the lichen finally reaches its full development. This indicates that the relation of the lichen to the alga is parasitism, as is its relation to the moss protonemata; but the algae are not so easily killed, and the lichen develops fully when it grows with them.

Nylander once thought that the algae were always free from the lichen hyphae, but later he abandoned this erroneous view. Schwendener (119) made the lichen a parasite and the alga a slave and preceded Warming in applying the term "helotism." He decided that the algae are seized, held firmly by the lichens and become so modified as to be identified with great difficulty if at all. Even such a filamentous alga as *Sirosiphon* parasitized by *Polychidium muscicolum* (Sw.) Gray, and *Rivularia* parasitized by species of *Lichina,* he proved to have the filaments broken up into groups of algae scarcely recognizable as belonging to these genera. He found *Scytonema* so modified, when parasitized by lichens, that he could not decide certainly whether it belonged to the Scytonemaceae or the Rivulariaceae. Much less did he claim any knowledge of the genus or the species. One can distinguish between *Rivularia* and *Scytonema* parasitized by lichens if the apices are normal, but this is very rarely, if ever, the case. Schwendener, in some instances, reached a conclusion regarding the species of the algal host by finding the free algae growing in proximity with the parasitized forms, or was able to distinguish the algae in very young lichens growing in groups of older lichens, which in turn were growing among the free algae. He records finding the algal host of *Pannaria brunnea* (Schw.) Mass., occurring in unrecognizable conditions in convoluted masses. These unroll, when boiled a moment in water or heated in dilute acid, into filaments of 100 or more cells, which belong to *Polycoccus punctiformis* or some closely related *Nostoc.*

The constancy of the dependence of the lichen upon the algal host has been much magnified by those who hold to the theories of mutualism or individualism. Frank was first (57) to note the long duration of growth of certain lichens independently of the host. His first statement was regarding the common *Arthonia radiata* (Pers.) Ach., which he found growing on bark a year or more without the alga, often remaining outside the parasitic relation until the apothecia were fully developed and the spores were forming in the asci. Then the algal filaments appear within the thalli, at first in small numbers, but soon become abundant. Again, Frank (58) records finding *Arthonia radiata* (Pers.) Ach. in its natural habitat, grown to large size without attacking *Trente-*

pohlia, the alga being parasitized later. The algal host enters the thalli from without. Then the thallus grows more luxuriantly and sometimes becomes partly epiphloeodal, though entirely hypophloeodal before parasitizing the alga. The lichen hyphae attack the *Trentepohlia* alga filaments, render them unrecognizable by breaking them up into shorter filaments or into single cells, and then according to Frank, bore into the cell contents of the individual cells. Whenever colonization fails, no apothecia are formed, the lichen (?) dying without fructifying. Frank found assentially the same condition in our common *Graphis scripta* (L.) Ach., which sometimes grows for a time outside the parasitic relation. He also found that *Arthonia dispersa* (Lam. & DC.) Dub. *A. punctiformis* Ach., *Arthopyrenia cerasi* Koerb. and *A. rhyponta* Mass. never enter into the parasitic relation with algae, the technique used showing no algae growing with any of these so-called lichens at any time. Frank studied only a few of the many similar lichens, and such tardy entrance of many of these plants upon the parasitic relation or entire failure to enter into this relation can scarcely be so rare as is claimed by those who adhere to the mutualism theory or some modification of it. These lichens and lichenoid plants are by no means rare and must be dealt with in any consideration of the relation of the lichen to its algal host. Frank found that the cells of the *Trentepohlia* filaments, when parasitized, show much thinner walls than when not parasitized, while the chlorophyll is absent or poorly developed. The oil globules are absent or of a golden or orange red color, while they are an intense rust red color in the free algae. He decided that the algal filaments bore through intact periderm as well as enter through cracks, and that these entering filaments arise from zoöspores which come to rest and germinate on the surface. He thought that the alga bored into the periderm only over lichen thalli; but this can hardly be true since *Trentepohlia* filaments commonly occur in the periderm where no lichens are growing. He observed that the alga resumes its usual form soon after the death of the lichen parasite.

Lindau (81) found that the points of contact between the hyphae of hypophloeodal lichens and the *Trentepohlia* filaments are comparatively few, and that no haustoria are formed. So

he thinks that the relation of these lichens to their algal hosts is a very loose one. In the fruticose *Roccellas,* the *Trentepohlia* cells are rent asunder and attacked by haustoria as are the usual palmelloid host cells in most higher lichens, but not so among the lower lichen parasites. It will be noted that Lindau does not agree with Frank regarding attachment of the hypophloeodal lichens to the algal host cells.

Frank found *Lecanora pallida* Schreb. to be of hypophloeodal origin, and to become epiphloeodal later. The unicellular algal host cells are always present over the central, thicker portions of the thalli. There is a marginal zone of hyphae, from which algal cells are absent. The algae occur singly and much scattered just inside of this zone, though tetrads may be recognized occasionally where the lichen hyphae have not pushed between the cells. These algal cells are, in part, pushed forward by the growing lichen hyphae and form new tetrads; the process is continued, and the host cells thus follow the growth of the lichen thallus laterally. Some of the algae are colorless, but are alive and divide actively. These colorless cells occur among normal green ones, but are absent from some thalli. Continued growth of the lichen and its algal host causes a breaking down of the periderm above, and lichen and host become epiphloeodal, except the marginal zone of the lichen, which remains hypophloeodal. After becoming epiphloeodal, the thallus acquires a pseudocortex of entangled hyphae, and the algal cells come to lie in groups below this cortex. Frank always found one or more cracks in the periderm of the area occupied by the young thalli. Through these he supposed that both the lichen and the algal host enter. He always found the algal cells in the cracks in the periderm. These are present and are attacked by the hyphae as they enter the cracks.

We may now pass to a consideration of some ideas regarding the physiological relations of the lichen to its algal host. De Bary (16) thought the lichen should be regarded the host and the alga a guest, treated with such great consideration that the relation should be regarded mutually beneficial. Reinke (65, 104 and 105) holds practically the same view and uses to express it the term "consortium," proposed by Grisebach (65). Schneider (109) also uses the term "mutualism" to express the relation of the lichen to

its algal host. Warming (140) uses Schwendener's term, "helotism," to express this relation. He believes that the alga grows and reproduces rapidly in the lichen through hypertrophy, a pathologic condition, and that it is hindered from zoöspore formation. Lindau (81) thinks that the lichen is parasitic on the alga, and that the many dead algal host cells result from lack of air and from the absorption of food by the lichen hyphae. Schneider's most extended statement (111) is to the effect that "in individualism is reached the acme of mutualistic association." He then proceeds to tell us that individualism requires that one of the symbionts shall be absolutely dependent upon the other, a condition which he thinks is found in lichens. He admits that the algal host may live without the lichen parasite, but thinks that since the lichen can not get on alone, it and the algal host together form a new physiological and morphological individual. He thinks that at some future time neither symbiont will be able to live alone, and that individualism will then have reached its acme. What fungus can get on well without its host? And what evidence have we, while the alga continues to thrive better alone than when parasitized, and while lichens are commonly found growing near the algae which they parasitize from time to time, that the algal host will one day be unable to live without the fungal parasite?

It is time to be done with these unproved and hopeless hypotheses of mutualism, consortism and individualism and turn to something more promising. In spite of all these hypotheses, the lichen is still parasitic, or more likely partly parasitic and partly saprophytic, on the alga. Those algal cells which are not invested or penetrated by lichen hyphae are usually of normal size and form and are darker green than those in the same thalli that are invested or penetrated by the hyphae. The lichen haustoria surely take from the algae foods which these algae have elaborated for their own nourishment. This must injure the algal host cells seriously and often kill them, for many of the algal cells in lichens are dead and devoid of protoplasm. The bright green cells which one finds in lichen thalli are those algal cells which have recently resulted from division. They are not yet parasitized, or have been parasitized but a short time. The results are the same

whether the hyphae enter the algal cells or not; but the injury to the host cells probably goes on more slowly in the latter case.

Peirce (98, 99) has decided in favor of parasitism of the lichen upon the alga, but inconsistently holds that the lichen and its host somehow form a dual organism in spite of this antagonistic relation. He found that while the algal host cells often multiply rapidly in lichen thalli, they increase yet more rapidly outside the lichens. During wet weather the alga grows more rapidly than the lichen; but during dry weather the lichen grows more rapidly than the alga. In this manner the algal host cells are preserved from complete extermination by the lichen parasite, though some host cells are constantly being killed. In parasitism on multicellular organisms, portions of the hosts are likewise often killed while new portions are being produced by growth. The cells of the unicellular or filamentous lichen hosts separate as they are formed, or constitute short filaments. The isolated cells or the filaments are not so able to overcome the harmful effects of parasitism as are the aggregates of cells in multicellular hosts, in which food supply may pass from cell to cell so that the cells on which the parasite feeds may be nourished from surrounding cells. But the algal hosts of lichens are by no means the only ones that are killed by parasites; nor are they the only ones in which the fungus kills only a portion of the host cells. Water, mineral salts, and probably some organic matter are carried to the imprisoned host. The parasite is not supposed to elaborate this material, more probably acting only as a carrier of food. Another peculiarity of the parasitism of lichens upon algae is that the algal hosts are usually surrounded completely by the parasite. Moreover, the lichen is usually parasitic on a large number of individuals instead of a single one.

Peirce says in his text-book of plant physiology (100) that "because of the small size of the alga, the always larger fungus can not become entirely enclosed in it; on the contrary, the fungus surrounds the alga with a more or less firm mycelium, containing the alga between the parts of its body. The association of the fungus and alga, always intimate enough for the fungus to supply itself osmotically with non-nitrogenous foods elaborated by the alga, is in many cases so exhausting to the alga that many of its

cells become entirely emptied. In spite of this evidence of complete parasitism of the fungus, some botanists claim that the alga is benefited also." We believe that this statement portrays fairly well the relation of the lichen to its algal host.

Elenkin has accomplished some very illuminating work regarding the parasitism or the saprophytism of lichens. He found (48) hyphae of *Lecidea atrobrunnea* (DC.) Schaer. piercing into the algal cells in most instances after the cells were disorganized and empty, but rarely into uninjured cells. He observed a similar relation between *Haematomma ventosum* (L.) Stein. and its algal host and felt uncertain about the rôle of the distorted hyphae found within the algal cells. He thought that the hyphae brought about probably through an enzyme, the destruction of the cell contents and finally of the walls of the algae for nourishment. Whether the lichen hyphae penetrate into the algal cells or work from the outside of the cell wall, he regards this method of nourishment endosaprophytism, since he thinks the role of the hyphae is to absorb dead rather than living matter. His second paper (49) enlarges on the first by treatment of a new series of lichens, but seems to add nothing otherwise. In a third paper (50) he states that his hypothesis is supported by the great abundance of dead algal cells in lichen thalli. He found that in thin sections stained carefully, the dead algae often exceed the living in numbers. He admits that death may be due to parasitism of the lichen on the alga, or to lack of air and light. In favor of the enzyme and endosaprophytism hypothesis he thinks is the presence of dead algae in greatest proportion in the haustorial zone, in which most of the algae occur. Here the lichen hyphae form a compact layer about the algae, so that the enzyme could easily deform and destroy the cells, which would then assume irregular shapes, while their protoplasts would become pale and disappear. Similar destruction of algae continues in the cortex, until the last vestige of algal protoplasts and walls are consumed, he thinks the latter at least saprophytically. Some algal cells remain rounded until after their protoplasts have disappeared. These are probably the ones that produce daughter cells vegetatively. Empty, dead algal cells surpass the living ones only in the haustorial zone of the thallus, while if reproduction ac-

counted wholly for dead cells, the living must here exceed the dead cells in number. So it is reasonable to suppose that the large proportion of dead cells in this region must be due mainly to parasitism or saprophytism. Elenkin thinks more probably the latter, the enzyme killing the algal cells, which are afterward absorbed. The dead cells are not wholly absorbed in the haustorial zone; but they are largely pushed into the cortex by growth, and there their consumption is completed by the lichen hyphae.

This absorption of dead walls, which Elenkin has observed in many lichens, it seems, must be carried on saprophytically, though the contents of the cells are probably consumed parasitically. Of course Elenkin's hypothesis, if true, makes mutualism a little more untenable, if possible, than does pure parasitism of the lichen upon the alga. He studied a wide range of lichen types and various kinds of algal hosts, and concluded that the hyphae, aided by the postulated enzyme, eat into the walls of the algal cells, not so much to obtain the protoplast within as to obtain food from the wall saprophytically. This makes the lichen, at least mainly, a saprophyte, on both the external, organic substratum and the enclosed algal host. Elenkin's hypothesis of endosaprophytism is far from proved, but the lichen is probably partly parasitic and partly saprophytic upon the algal host. Whether the hypothesis is valid or not, its author has placed before us a series of facts regarding the relation of the lichen to its algal host which must provoke much careful investigation and has added materially to a solution of the problems involved.

Danilov (46) found that a hypha enters the algal protoplast, and branches into a delicate network of slender hyphae, which penetrate through the protoplast in various directions. The walls of the hyphae of this network are very thin and can be seen only with great difficulty. One also finds in the algal cells hyphae like those of other portions of the lichen. These occur alone, or with the slender hyphae, one or both kinds filling the entire space within the cell. Danilov thinks that the slender hyphae pass into the ordinary kind, after absorbing the contents of the cell, grow out of the protoplast and attack other algal cells in similar fashion. Through the effects of the slender branched hyphae, the algal cells are deformed and finally killed. He often found the protoplast

shriveled and irregular in form, gradually disappearing and replaced by the larger hyphae. During this process, the algal cells become pale, and many empty cell walls also remain. In an early stage of parasitism of a hypha on an algal cell, when the hypha has just become appressed and enlarged, the algal cell is irritated and divides rapidly, forming new cells, which are free for a time. These are later attacked by the lichen hyphae. Danilov makes nothing of Elenkin's theory of endosaprophytism, but thinks rather that the lichen is purely parasitic on the alga. Of course the relation is wholly antagonistic in either case.

Treboux (134) in a more recent research thinks it hardly supposable that the lichen receives any considerable portion of its organic material from the algal host, or that the alga depends upon the lichen to any appreciable extent, even for carrying water, mineral salts or organic food from the substratum. He thinks it much more probable that the alga obtains both moisture and nourishment mainly from the air. He mentions Beijerinck's work on algae supposed to obtain carbon from peptone compounds and states that *Cystococcus humicola* belongs here and is the host of many lichens. He thinks there are really no peptone algae but rather that most algae can get their carbon from peptone compounds under certain conditions, and from the air under other conditions. So an alga may have one source of carbon when serving as the host for a lichen and a very different one when free, and the lichen may lay hold of free *Cystococcus humicola,* which will at once change its method of nutrition. If this be true, it is no longer necessary that we should think the method of nutrition changed through long living with a lichen. After comparing the *Cystococcus* forming lichen hosts with other algae, he concludes that it is an independent species, distinct from both *Chlorococcum* and *Pleurococcus.* Neither the free *Cystococcus* nor specimens recently isolated from lichen thalli is much given to zoöspore formation. The free-living *Cystococcus humicola* shows the same characters as the lichen host, except for modifications caused by parasitism, and quickly assumes the usual form and method of nutrition when freed. Both the free algae and those recently liberated from lichen thalli readily pass into the hostal relation with lichens in cultures. The alga grows and reproduces much more

rapidly in free nature than in lichen thalli, where it shows a sickly, unnatural appearance, seen in the paler color, the less refractive condition of cell contents, and the common absence of the pyrenoids, all of which indicate parasitism of the lichen upon the imprisoned alga. The injurious effects of the lichen upon the algal host are greatly lessened, he finds, when the lichen and its host are grown together on a favorable nutrient medium, where the lichen can secure more of its nourishment from the substratum, and so depend less upon the host. Treboux's conclusions, though based upon rather limited investigation, seem reasonable, are in accord with other recent results and demand a modification of some views commonly held concerning the relation of the lichen to its algal host. For instance, the lichen may at any time readily lay hold of free algae, an entirely reasonable supposition, which deals a death blow to certain untenable suppositions regarding the nature of lichens. According to his view also the food relation of the lichen to its algal host is not a very close one; but his results at this point are not based on careful investigation, and we are still disposed to believe that higher lichens depend largely upon their hosts for food. Whether *Cystococcus humicola* is distinct from *Chlorococcum* is a problem very difficult of solution, and judgment may well be reserved, especially as this question scarcely affects any important matters concerning the relation of the lichen to its algal host.

C. E. Bessey (22) says in "The Essentials of Botany," "The plant body of a lichen is composed of jointed, branching, colorless filaments similar to those in the other families of this order, but more or less compacted together into a thallus or branching stem. They obtain their nourishment from little green protophytes or phycophytes to which the filaments attach themselves parasitically. These little hosts, which live in the midst of the moist tissues of the lichens, were until recently supposed to be parts of the lichen itself. . . . There is thus an association between these plants which is mutually beneficial (symbiosis). The lichen lives parasitically upon the green plants, to which it in turn furnishes shelter and moisture." Clements in his text (36) defines thus: "The type of parasitism in which the presence of the parasite benefits the host plants in some measure is commonly distinguished as sym-

biosis or mutualism." The views of Bessey and Clements seem identical, though couched in somewhat different terms. Clements' definitions of parasitism and symbiosis, like Bessey's statement, are unusual, but both admit of the use of the term, parasitism, in designating the relation of the lichen to its algal host, even by those who believe in mutualism of the extreme form known as individualism. But parasitism and mutualism, as usually defined, can not be said to exist at the same time between two plants in symbiotic relation. The symbiotic relation must be antagonistic, as in parasitism, or mutualistic, as in mutualism. We admit that the algal host may be benefited in some ways by the association with the lichen; but since the injury received is, as a whole, greater than the possible benefit, the relation is parasitism, or antagonistic symbiosis.

THE RELATION OF THE LICHEN TO THE SUBSTRATUM

Some lichens grow on certain kinds of rocks and others on other rocks; some on barks of certain trees and others on barks of other trees; some on decorticate wood still intact and others on rotten wood; and some on one kind of soil and others on other kinds. Hence, it is reasonable to suppose that lichens secure some nourishment from their substrata rather than to think that their distribution upon various substrata is governed entirely by physical structure of these substrata. Moreover, we can not understand the relation of the lichen to its algal host without considering the relation to the substratum; hence, a summary of knowledge upon this subject must be given in this paper.

Schwendener (117) in his epoch-making studies of the thalli of lichens paid little attention to the lichen rhizoids, but reached the general conclusion that they do not, in higher lichens, penetrate into the periderm to any considerable extent. Lotsy (84) studied the rhizoids of a number of foliose lichens and found them spread out on the substratum; he thought none of them penetrated below the surface. Frank (58) and Bonnier (31) decided that lichen hyphae and *Trentepohlia* filaments are able to penetrate into periderm cells and extract food from the walls and the cell contents. Lindau (81) found that these earlier workers were mistaken, and that the algae, and the lichen hyphae of hypophloeodal lichens,

only pass between the periderm cells, which they often force apart, but never enter. As the periderm layers are forced apart by the lichen hyphae and the accompanying algal filaments, they come to lie in irregular, isolated masses, with large areas of lichen and algal host tissues lying between. Both lichen and alga enter the bark through microscopic cracks and spread laterally in the periderm, the lichen preceding and the alga following and helping to fill the spaces produced by pushing the periderm layers apart. All ascomycetes found in periderm work in the same manner, and one can scarcely study sections of any bark of considerable age, without finding hyphae pushing between periderm layers, sometimes reaching as deep as the fortieth layer.

Cooke (39) found that cinchona bark, when it supports luxuriant growths of lichens, abounds in the medicinal alkaloids characteristic of this tree, while these substances are largely destroyed by other fungi, which may thrive in or on the bark. This would indicate that lichens secure little nourishment from the substratum. Even if Cook's findings are reliable for epiphloeodal lichens, they can scarcely be true for hypophloeodal lichens, which are loosely combined with their algal hosts, some of them living for years in the periderm before attacking an algal host.

It is certain that hypophloeodal lichens which live in the periderm for a year or more outside the relation with an algal host must take nourishment from the periderm, though they do not dissolve sufficient material from the periderm walls to be detected by microscopic examination. So we must believe that these plants secure nourishment from the periderm without entering the cells or producing appreciable diminution in walls or other effects that can be detected without chemical analysis.

The rhizoids of our common *Buellia parasema* (Ach.) Koerb. and our *Rinodina sophodes* (Ach.) Koerb., both epiphloeodal crustose lichens, penetrate through openings to a depth of five or six layers of periderm and spread out between these layers. Lindau (81) found that such foliose lichens as *Parmelia physodes* (L.) Ach. and *Physcia stellaris* (L.) Nyl. surround and penetrate into all elevations of the periderm and also fill the depressions closely. They are often confined wholly to these surface elevations and depressions, but sometimes penetrate between the

outer, loose layers of periderm. They never bore between firm layers of periderm as do the crustose epiphloeodal and the hypophloeodal lichens.

Evernia prunastri (L.) Ach. is attached to the substratum by a broad, basal holdfast, which becomes larger as the lichen grows. Lindau (81) found the plant often attached to lenticels, through whose loose tissues the rhizoids penetrate and also extend a short distance into the surrounding periderm. When this plant grows on older branches, the holdfast penetrates into the periderm and spreads about between the layers, which are finally separated so that masses of hyphae come to lie between them. The rhizoids may penetrate at least to the tenth layer of periderm. The separated layers become thinner as they are pushed outward by the penetrating hyphae, until they are finally only about half their original thickness. The thinning does not indicate that the hyphae have dissolved material in the walls of periderm cells, for if this were true, the hyphae would be able to penetrate through the cell walls. As the periderm layers are carried upward, they come in contact with the atmosphere, which doubtless dissolves the walls. However, it is reasonable to suppose that the air produces some change in the composition of the periderm fragments such that the lichen hyphae may be able to dissolve and appropriate the transformed product, thus securing food and aiding in the thinning process. Lindau observed the same thinning of periderm fragments in which some crustose lichens were growing.

Hypophloeodal lichens, especially those that live a long time outside the relationship with an algal host, must secure a large amount of nourishment from the periderm, with which their whole thalli come in contact. The epiphloeodal crustose species are in closer contact with their algal hosts and less closely attached to the bark. Hence, they must secure more nourishment from the alga and less from the substratum. The foliose lichens enclose numerous algal host cells and are much less closely attached to the substratum than any crustose forms, being above it, while their rhizoids penetrate but a short distance into it, so these must depend still more upon the algal host and less upon the substratum. Fruticose forms are still less closely

attached to the substratum, being fastened usually at one point only, and are, of all lichens, least dependent upon the substratum and most dependent upon the algal host for their nourishment. In general, as the proportion of bulk of the lichen above the substratum increases, the penetration into the periderm decreases, and the lichen becomes more and more dependent upon its algal host. In other words, the lower the lichen, the more dependent upon the substratum and the less dependent upon an algal host; and the higher the lichen in the scale of development, the less the dependence upon the substratum and the greater that upon the algal host. Since the proportion of contact with the substratum decreases as we ascend the scale of lichen development, the higher lichens can hardly carry large amounts of nourishment to the algae within them. The evolution of lichens has involved a gradual change in food supply, and these plants have become more and more dependent upon algal hosts.

The substratic relation of lichens growing on decorticate wood are much like those of epiphloeodal forms on bark, whether the lichen be crustose, foliose, or fruticose. Lindau (81) investigated *Biatorina synthea* (Ach.) Mass. on decorticate pine wood. The thallus and the algal host lie among the tracheids, which become corroded and sloughed off, while the algal cells lie in the cavities thus formed. The lichen hyphae penetrate between the tracheids and push them apart. Then the alga enters, and one finds in section a mass of tracheid fragments, lichen hyphae and algal cells, all of which are sloughed off above as the lichen and the alga penetrate deeper into the wood. The lichen hyphae pass into the tracheids and medullary ray cells, through broken down bordered pits and thus bore deeper and deeper into the wood.

Psora ostreata Hoffm. sends its rhizoids through holes into the rotten pine wood on which it grows, and the hyphae enter the tracheids through broken down bordered pits. They pass from tracheid to tracheid, and penetrate into medullary-ray cells through similar pits, thence deeper into the wood. Both tracheids and ray cells are often filled with rhizoids. *Cladonias* on top of stumps of coniferous trees easily send their rhizoids to unusual depths, entering the cut ends of tracheids, thence passing from

one tracheid to another through the broken-down bordered pits and thus deeper and deeper into the wood.

The substratic relation of lichens that grow on the epidermis of twigs or leaves are peculiar and indicate a very limited dependence, if any, upon the substratum. This points to a pronounced dependence of the lichen upon the algal host. Lindau (81) examined *Biatorina bouteillii* (Desm.) Lind. on the upper surface of fir leaves, where the plant forms a continuous layer. The lichen can be removed easily, since the thallus does not penetrate into the leaves. This agrees well with Ward's (138) results with *Strigula,* which he found growing superficially on tropical leaves, not even attached by haustoria. It may well be doubted whether these lichens receive any nourishment from the leaves on which they grow. It is more probable that they depend wholly upon their algal hosts for food supply. Lindau (81) also studied the foliose *Xanthoria parietina* (L.) Th. Fr. on leaves of *Abies pectinata.* The lichen is closely attached to the leaves by its rhizoids and covers the whole surface. The rhizoids even fill the vestibules of the stomata, but do not enter the tissues of the leaves, which are killed, probably by suffocation. On the bark of the same tree, the rhizoids of this lichen pass through a few layers of the loose periderm. If this lichen can live on leaves without securing food from them, it and other foliose and fruticose lichens should be able to live in the same way on barks.

Fitting (56) decided that certain lichens penetrate into the tissues of leaves and injure or even kill them. He thought that many more might dissolve the cuticle, while a few spread over the surface of the leaf without affecting it in any way. There is no real conflict in this, with the views of Ward and Lindau; for Fitting regarded the alga part of the lichen, and it is the algal host that bores into the leaf before it is attacked by the lichen. The latter is thus brought into a position where it may extract food without itself boring into the leaf, which is often killed where attacked by the algal host, even before the latter is parasitized by the lichen. It is also the alga that dissolves the cuticle, or works its way under this structure and spreads out between it and the epidermis. The *Trentepohila*-like alga is often seen

living alone under the cuticle. Fitting found that the algal host could bore into some leaves and not into others, so the relation of both alga and lichen to the leaf would vary. Since the leaf is injured only where the alga attacks it and is often irritated into an unusual thickening of epidermis and palisade and a development of suberin at the points affected, it would not be reasonable to ascribe the results to the lichen, which may, however, have a part in working injury where present.

When *Parmelia olivacea* (L.) Ach. grows on small limbs that have not lost their epidermis, the rhizoids branch centripetally below into a hyaline layer of branches, which completely and closely cover the epidermis, but remain wholly superficial. A form of *Physcia stellaris* (L.) Nyl. on the perennial leaves of *Abies pectinata* also forms a complete hyphal layer over the leaf surface, but the rhizoids do not penetrate into the leaf. The lichen is easily separated from the leaf, and the hyphal layers forms a complete negative of the leaf surface. On young branches of the same tree, with epidermis still intact, Lindau (81) found the the leaf and adhered closely to the upper halves of the trichomes that the rhizoids reached only half way down to the surface of ~~the leaf~~ and adhered closely to the upper half of each trichome and to organic and inorganic particles lying between them. If the leaves or the young branches were killed by the lichen, or showed signs of injury, it would seem likely that the closely applied rhizoids might secure food from these surfaces, or from the trichomes. In the absence of such evidence, it appears probable that these lichens do not secure food from the substratum.

Winter (142, 143) seems to have been first to study the relation of lichens to the rocks on which they grow. He found lichen rhizoids penetrating into the rocks to considerable depths and ascertained that the rock can be dissolved with fluoric acid, when the whole rhizoid system appears, and the relation of the lichen to the algal host can be seen plainly. Egeling (47) found that a glass surface on which a lichen was growing became covered with minute cracks, in which were organic and inorganic particles from which the lichen could secure nourishment. Glass is known to be soluble in carbonic acid, and the algal hosts are

probably able to form this substance in the process of carbon assimilation; hence, the surface of the rock would, in time, become corroded so that the lichen hyphae could penetrate into it. Bachmann (12, 13) has since concluded that lichens neither corrode nor penetrate into quartz or silicates; but Stahlecker (125) proved by careful observation that lichen hyphae will penetrate into all rocks, after they have been corroded as explained above.

Zukal (149, 150) studied the sphaeroidal cells and the enlarged hyphae found in lichens on calciferous rocks. By subjecting these structures to careful chemical treatment, he ascertained that they contain a fatty oil similar to that found commonly in fungal spores and sclerotia. He decided that the oil must be a reserve food supply elaborated by the algal host. Fünfstück (63), by removing the algal host and the upper portion of the lichen thallus from the rock, proved that the hyphae still remaining in the rock continue to grow for two or three years without the algal host and produce the sphaeroidal cells and the enlarged oil-bearing hyphae as well as before. He thus proved positively that the algal host plays no part in the oil production, and decided that the oil is not a food but a waste product, of no use to the lichen. He has proved the first point, but not the second.

Bachmann (8, 9, 10) studied the relation of certain lichens to the dolomite and the limestone on which they grow, by dissolving fragments of the rock and by grinding pieces of rock into thin sections, in which the lichen and its algal host cells could be seen. He found that these lichens of calciferous rocks are usually hypolithic, only the fruits showing at the surface. The lichens he found to penetrate from 200 to 12,000 or 14,000 mic. into the rock, while the algal cells reach depths of 100 to 500 mic. Each algal group is surrounded closely by lichen hyphae; but neither Bachmann nor other workers has found out more regarding the relation of the lichen to the algal host in these or other rock-inhabiting lichens. The hyphae eat their way into the rock without respect to structure, passing through crystals of various forms and sizes. In support of the belief that the oil is reserve food, Zukal claimed that lichens that grow on bark, on earth and on rocks devoid of lime or magnesia contain the same kind of fatty oil, sometimes in as great abundance as those that

grow on calciferous rocks. He thought that the oil must be produced with little regard to the amount of lime in the substratum, while Fünfstück, who regarded the oil a waste product, failed to find it in considerable quantity, except in lichens that grow on calciferous rocks. Bachman agrees with Zukal, while Friederich and Stahlecker agree with Fünfstück. Those who regard the oil a reserve food, think that it is most abundant about the time that the lichen fruits begin to form, while Fünfstück found it quite as abundant at other times and in lichens that produce little or no fruit.

Bachmann (11) also worked on the lichens on silicious rocks and found that the rhizoids usually penetrate through the mica particles of granites, commonly passing between the lamellae, but sometimes passing through them. He found the oil-bearing sphaeroidal cells, but performed no careful chemical analyses to prove that lime is not present in some of these rocks in sufficient quantity to account for their presence. As stated above, Bachmann concluded that lichens do not attack quartz and silicates chemically; but it has been proved that they or their algal hosts secrete acids which do corrode these rocks so that the lichen hyphae penetrate into them. It is certain that moisture, oxygen, carbon dioxide and carbonic acid are rather abundant about lichens because of the nutritional processes of the lichens and their algal hosts, and one or more of these agents will dissolve any rock.

Stahlecker (125) subjected rocks to careful chemical analysis and found that ordinary statements about the character of rocks on which lichens grow are very unreliable, and that there is really a close relation between the oil secretion and the amount of lime and magnesia present in the rocks. Friederich (59) ascertained that lichens attack all rocks, but lay hold on the more basic portions sooner than the more acid. This would account for finding certain portions of granites attacked and others left bare for a time, but does not warrant the conclusion of Bachmann that some rocks are not attacked at all.

In general, the more the lichen penetrates into the rocks the less numerous are the algal host cells, and the less the penetration into the rock, the more abundant the algal cells. So the quartz and

silicate inhabiting lichens, which are mainly epilithic, are poorly developed, while their algal host is strongly developed. Lichens that grow in the calciferous rocks are strongly developed, and the algal host cells are not abundant. This favors the view that the more intimate the relation of the lichen to the rock, the less its dependence upon an algal host. This again favors the conclusion that the oil is a reserve product and accords with our finding that, in bark-dwelling lichens, the closer the relation to the substratum the less intimate that with the algal host. Fünfstück (63) found that the more abundant the algal host cells, the less the amount of oil present; and this, with his other findings given above, makes our conclusion practically certain.

It may seem that we have gone far afield in discussing at some length the relation of the lichen to its algal host and to the substratum. For the writer and some others, this would not have been necessary in the present series of papers, for some of us believe that the lichen is a fungus, whatever its relation to the algal host. But for others, the traditions would not be abandoned without proving that the lichen is a parasite, or perhaps partly a saprophyte as well, on the alga. As stated above, it will be seen that the relation of the lichen to the algal host can not be understood until we also have before us the facts regarding its relation with various substrata. Hence, we have given a summary of knowledge on these points and are ready to treat, in the next paper, the classification of lichens, with the matter of their nature thoroughly considered.

SUMMARY AND CONCLUSIONS

1. There has been hitherto no agreement regarding the nature of the lichen, and the only thing about the problem generally believed by botanists is that the green and the blue-green cells in lichens are algae.

2. Due probably to clinging to traditional phraseology, most botanists are not able to express themselves consistently with respect to any view that they may hold relative to the nature and the proper treatment of lichens.

3. The text-book statements about lichens are rarely coherent, excepting those that cling to an entirely traditional and erroneous position.

4. The fundamental problem concerns the nature of lichens, and this must be settled before we can hope to agree regarding the classification of these plants.

5. Due to peculiar ideas about the relation of the lichen to its algal host, this problem of relationship has become the main part of the consideration of the nature of the lichen. It is therefore treated at length in this paper.

6. Recent researches prove that all hypotheses of mutualism between the lichen and the symbiotic alga are erroneous, and that the lichen is a fungus pure and simple.

7. The following are the main arguments against mutualism. Lichens commonly grow where there are free algae of the same species as those parasitized by these lichens. The spores of the lichens germinate and attack the free algae as other fungi attack their hosts. Lichens perform like other fungi on culture media and may be made to produce their reproductive organs on these media. Their development on such media does not differ from that reached when growing with their algal hosts more than other fungi vary from their usual appearance when grown on culture media. Lichen spores also attack the algal hosts, when the spores and the algae are introduced into cultures together; and the resulting lichen is normal and sometimes fructifies in the cultures. Algal hosts extracted from lichen thalli grow in cultures like free algae of the same species grow on similar culture media. Some lichens live for years in their substrata outside the relation with their algal hosts. The researches of Elenkin and Danilov prove that lichen hyphae absorb food from the algal host cells, which are killed by severe parasitism or more probably by parasitism and saprophytism combined. The relation of the lichen to its substratum proves that higher lichens can take comparatively little food from it and must depend more than lower lichens upon the algal hosts; and this shows that the parasitism of the lichen upon the algal host has become more severe in the evolution of higher lichens. Finally, the algae parasitized by lichens are in a disadvantageous position with reference to carbon assimilation.

8. The following are the main arguments for the fungal nature of lichens. Lichens are like other fungi with respect to vegetative

structure and fruiting bodies. The bridges which connect lichens with other fungi are not few but many. Since it is thoroughly demonstrated that the lichen is parasitic, or partly parasitic and partly saprophytic on the alga, there is no longer even a poor excuse for a "consortium" or an "individualism" hypothesis.

9. The parasitism of lichens on algae is peculiar in that the unicellular or the filamentous hosts are usually enclosed by the parasite, which may carry more or less food material to its host. The host inside of the parasite is placed in a disadvantageous position with reference to carbon assimilation and may depend, for its carbon supply, more or less upon material brought from the substratum by the parasite. Some algal individuals not yet parasitized may be found in most lichen thalli.

10. *The lichen is a fungus which lives during all or part of its life in parasitic relation with the algal host and also sustains a relation with an organic or an inorganic substratum.* The definition may need modification later to recognize Elenkin's hypothesis, in part or fully.

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THE PROBABLE IDENTITY OF STROPHARIA EPIMYCES (PECK) ATK. WITH PILOSACE ALGERIENSIS FRIES

Edward T. Harper

While making notes on the species of *Stropharia* reported from this country to accompany some photographs soon to appear in the *Transactions of the Wisconsin Academy of Sciences,* my attention was called by my brother, Prof. R. A. Harper, to the fact that Lanzi's figures of *Pilosace algeriensis* Quél. (Fungi Mang. *pl. 67. f. 3*) closely resemble *Panaeolus epimyces* Pk. or *Stropharia coprinophila* Atk. The drawings by Miss Helen Sherman (Jour. Myc. **11**: *pl. 80*) and the photographs by Prof. Atkinson (Plant World, June, 1907) show a striking resemblance to Lanzi's figures and a comparison of the published descriptions confirms the evidence of close relationship between the European and American plants. The size and shape of both plants is the same, pileus 1–2 inches broad, stem 1–2 inches long, up to ½ inch thick. The stem of the European plant is solid or stuffed, that of the American plant is the same, becoming hollow when old. The pileus and stem in both plants are whitish and silky. Both have purplish-brown or blackish spores. Peck gives the measurements $5–6 \times 7.5–9\,\mu$. Miss Sherman says the spores are slightly larger, up to $7 \times 10\,\mu$. Atkinson gives the measurements $3.5–4.5 \times 7–8\,\mu$; Lanzi $5.5 \times 6.5–7\,\mu$, and describes them as inequilateral or slightly reniform. Quélet reported the spores as subsphaeroid, $8\,\mu$ in diameter. The greatest difference appears to be in the reports as to the attachment of the gills. Lanzi says the gills are distant from the stem and free. Peck described them as rounded-adnexed. Atkinson says the gills are adnate to adnexed, slightly sinuate or rounded, and he places the plant in the genus *Stropharia,* but reports the stem as separating easily from the pileus, which is a character of plants with free gills.

The comparison proves the very close relationship of the two

plants. The differences are no greater than might be expected in plants from such widely separated localities. In some characters, such as spore measurements, Peck and Lanzi agree better than Peck and Atkinson. Lanzi does not describe his plant as a parasite nor recognize the "tuberous mass" at the base of the stipe as an abortive host. His figures, however, leave no question as to the identity of the parts in the two forms. His interpretation of the cleft which appears in the vertical section of the basal bulb is erroneous. Such a cleft could not possibly have anything to do with the formation of a ring and it has been recognized by the American students of the material with entire unanimity as representing the gill cavity of the host. In the Madison material, rudimentary gills and ripe spores of the *Coprinus* are found in this cleft. Lanzi also misinterprets his figure *c*, which must have been based on a mature stage of the plant with a very short stipe. Lanzi regards the fungus as rare and apparently neither he nor Quélet ever collected it personally.

The American plant was first described as *Panaeolus epimyces* Peck (Rep. N. Y. State Mus. **35**: 133–134). Dr. Peck left the host plant undetermined. Atkinson described the same plant independently, naming it *Stropharia coprinophila*, and determined the host plant as *Coprinus atramentarius* (Jour. Myc. **8**: October, 1902). Mr. F. E. McKenna and Miss Helen Sherman studied the plant at Madison, Wisconsin, and determined the host plants as *Coprinus atramentarius* and *Coprinus comatus* (l. c. *107–169*. 1905). Prof. Atkinson has written a second paper on the plant in which he admits the identity of his plant with *Panaeolus epimyces* of Peck, but holds that it is a *Stropharia* and names it *Stropharia epimyces* (Peck) Atk.

The European and American forms certainly belong to a single group, including *Pilosace algeriensis* (Fries) Quél. (Fl. Jura Vosg. 351), *Panaeolus epimyces* Peck, and *Stropharia coprinophila* Atk. The common method followed by Atkinson when he made the combination *Stropharia epimyces* (Peck) Atk. results in the burying of much information about it. Atkinson wrote a new description of the plant and when this is compiled in the *Sylloge* or a manual the student cannot know that other spore measurements than $3.5–4.5 \times 7–8 \mu$ have been observed; that the gills

have been found simply adnexed instead of adnate to adnexed, etc. The collector of plants like those found by Peck or Miss Sherman, who attempts to use Atkinson's description, will find himself in a predicament understood by everyone who has attempted to identify agarics from descriptions.

An interesting result of Lanzi's work in making *Pilosace algeriensis* known in Europe is that Cooke's illustration of that species in his plate 618 is shown to rest on an incorrect determination. The figure has been copied far and wide as an illustration of the genus. Lanzi suggests that it may be based on an exannulate form of *Agaricus campestris* such as that figured in Cooke's plate 528.

GENESEO, ILLINOIS.

NEWS, NOTES, AND REVIEWS

Dr. B. T. Galloway, chief of the Bureau of Plant Industry since 1900, has been appointed Assistant Secretary of Agriculture by President Wilson, and Dr. W. A. Taylor succeeds him as chief of the Bureau.

Mr. Stewart H. Burnham, for some years assistant to the state botanist at Albany, resigned on April 1 on account of ill health. His address is now Hudson Falls, New York.

Dr. E. A. Burt, professor of natural history in Middlebury College, Middlebury, Vt., has been appointed librarian and mycologist of the Missouri Botanical Garden. The appointment will date from next September.

Professor L. H. Pennington, of Syracuse University, and Dr. Gertrude S. Burlingham spent the Easter holidays at the Garden consulting the mycological herbarium and library in preparation of manuscript for a forthcoming part of NORTH AMERICAN FLORA.

The first number of *Phytopathology* for the current year contains, in addition to several important contributions, a full account of the Cleveland meeting of the American Phytopathological Society with abstracts of the papers presented. The editors are to be congratulated upon the decided improvement in the general appearance of this periodical.

A valuable collection, containing several hundred specimens of fleshy and woody fungi, has been recently obtained for the Garden herbarium from Femsjo, South Sweden, by Mr. Lars Romell, probably the best Swedish authority on these groups of plants. Specimens from this locality are especially interesting on account

of the studies made there by Elias Fries in the early years of his life.

SHEAR'S STUDIES OF PARASITIC SPECIES OF GLOMERELLA

"Studies of the fungous Parasites belonging to the genus *Glomerella*," by Dr. C. L. Shear, appears as Bulletin 252 of the Bureau of Plant Industry of the United States Department of Agriculture. The name *Glomerella* is the generic name applied to the ascogenous stage of *Gloeosporium* or *Colletotrichum*, which attacks various kinds of plants giving rise to a variety of diseases.

The object of the paper as set forth by its author is to determine the life histories, habits and identity or relationship of the forms of *Gloeosporium* or *Colletotrichum* found on the same or different hosts. The paper covers the investigations of members of this group of organisms obtained from 45 host plants. Of the 473 species of *Gloeosporium* and *Colletotrichum* given by Saccardo not including members of the genus included by Saccardo under other generic names, it is estimated by Shear that about 50 per cent. of these so-called species cannot be determined except on the basis of host relations or the part of the host attacked.

The life history of forms from 36 different hosts plants have been determined and recorded in this paper, 17 having been produced in pure culture and 19 on the host either in moist chamber or under natural conditions. All of the material from the 36 hosts is referred to three species, *G. cingulata, G. Gossypii,* and *G. lindemuthianum,* the first occurring on 34 hosts and the remaining two on one host each.

None of the morphological or physiological characters in the genus seem to be well fixed, the conidia, chlamydospores, perithecia, ascospores, and paraphyses showing a wide range of variation. Most forms do not seem to be restricted to any particular host.

The question is raised as to why the life cycle of *Glomerella* and other pyrenomycetes is sometimes completed in pure culture while at other times only conidia or pycnospores or no fructification of any kind is found. Various views on this subject have been summarized but the question is still an open one for *Glom-*

erella although some of the supposed factors have been tested sufficiently to eliminate them.

F. J. SEAVER.

RIDGWAY'S NEW COLOR GUIDE[1]

A new color guide by Dr. Robert Ridgway, the well-known ornithologist, is practically an entirely revised and much enlarged edition of his earlier nomenclature of colors (1886) with 17 plates and 186 colors as against 53 plates and 1,115 colors in the present work. The color work was done by A. Hoen & Co., of Baltimore, and is much more uniform in different copies than in the earlier edition, which was hand stenciled from several mixings of the same color; while in the present work each color for the whole edition of 5,000 copies was prepared from one lot of color and uniformly coated at one time. While the present work does not contain quite as many colors as are included in the more bulky French work by René Oberthur, the gradation between colors is more uniform, and the colors are on dull instead of glossy-surfaced paper as in that work, which gives a slightly different, but more natural color effect, and no metallic color effects are included. The proportion of darker broken colors is greater, which will appeal especially to the ornithologist and mammologist, although the work is designed to be equally useful to botanists, florists, artists, dyers, merchants, and chemists who require a standard color scheme. The colors have evidently been standardized to a degree of accuracy not hitherto attained in any color chart. The colors are one-half by one inch, arranged on a heavy gray paper in three vertical columns of 7 colors each. The plates are divided into 6 series. In plates I–XII the middle row of horizontal colors represents the 36 colors and hues most readily distinguished in the spectrum, although it is said to be possible to distinguish 1,000. Above these colors each succeeding horizontal row of colors is the spectrum color mixed with 9.5; 22.5; and 45 per cent. of white. Below they are mixed with 45; 70.5 and 87.5 per cent. of black. Plates XIII–XXVI represent the colors in

[1] Color Standards and Color Nomenclature. By Robert Ridgway [3447 Oakwood Terrace, N.W.], Washington. Published by the author 1912. Pp. 1–44; pls. I–LIII. $8.00.

plates I–XII dulled by 32 per cent. of neutral gray; plates XXXII–XXXVIII are dulled by 58 per cent. of neutral gray; plates XXXIX–XLIV are dulled by 77 per cent. of neutral gray; plates XLV–L are dulled by 90 per cent. of neutral gray; and plates LI–LIII are dulled by 95.5 per cent. of neutral gray. If the color to be matched is darker than in the first series of plates, turn to the same position in the succeeding 5 series of plates until one is found that is dark enough to match. This is readily done by referring to the numbers at the head of the vertical columns and to the letters at the left of the horizontal rows. In numbering and lettering the rows of colors, every other number and letter has been omitted so that colors that do not exactly match any in the present work, but are intermediate, can be designated by a symbol. For example, in plate I the vertical columns are 1, 3, and 5; the tints b, d, and f; and the shades i, k, and m. All the colors are named as well as symbolized, but if a given color comes between Hermosa Pink (1 f) and Eosine Pink (1 d) it could be designated 1 e. In this manner about 2385 additional colors or a total of 3500 can be designated. Undoubtedly exception will be taken to some of the names, but in this the personal equation plays such a large part that decisions must be rather arbitrarily rendered. The primary colors have been standardized by Dr. P. G. Nutting, of the U. S. Bureau of Standards.

It was originally expected that six months would suffice for the preparation of the colors, but unforeseen difficulties in reproduction have extended this period to about three years.

A list of color synonyms as shown by the immense list of trade samples that must have accumulated would have formed an exceedingly interesting and valuable addition to the work.

A table of percentages of color, together with an explanation of the amount of white, black, or neutral gray used as above, will give an approximately ready clue to the reproduction of any color in the guide, the only uncertain factor being the possible lack of standardized primary colors with which to begin.

Definitions of the principal color terms, such as color, shade, tint, hue, tone, etc., which are used almost interchangeably by many people, will repay careful study by those not familiar with their exact use.

A slight error on page 12, due to a misunderstanding, should be corrected. Mr. F. A. Walpole had no connection with the color project of the American Mycological Society, the preparation of which was delegated to the late Dr. L. M. Underwood, Dr. W. A. Murrill, and the writer. Mr. Walpole died before the committee was appointed, and the project was abandoned after two years' work by the committee in favor of Dr. Ridgway's work, which had not previously come to their notice.

P. L. RICKER.

FAULL'S CYTOLOGY OF THE LABOULBENIALES

Faull[2] has recently published an account of his cytological studies upon two species of the Laboulbeniaceae found on the elytra and on the free tip of the abdomen of the common whirligig beetle. The species, *Laboulbenia chaetophora* and *L. Gyrinidarum,* are closely related forms and are not easily distinguished in the young stages. Both species are apogamous, nothing resembling antheridia being found, although a much-branched multicellular trichogyne is present in each species. Thaxter's account of the general morphology of species of the genus are confirmed in a number of points.

The methods in ordinary use for fixing and imbedding fungi were employed. The septa between the daughters of the same mother cell are single pitted, and a continuous protoplasmic tract extends through the receptacle to the tips of the appendages. No broad protoplasmic bridges, however, are to be found between the cells of the receptacle. The protoplasm which dips into the opposite lying pits is in reality separated by the thin middle lamella which is perforated by one or more minute pores. Only very fine strands, plasmodesmen, connect the cells. The septa in the appendages are apparently coarsely perforated, so that the cytoplasmic fibrils extend out from the pits in the cells of the receptacle, and occasionally similar strands are seen leading out from the nuclei. Their function has not been determined except that

[2] Cytology of the Laboulbeniales, Ann. Bot. **25**: 649–654. Jl. 1911: The cytology of *Laboulbenia chaetophora* and *L. Gyrinidarum.* Ann. Bot. **26**: 325–355.

in disintegrating cells they are very persistent elements of the cytoplasm.

The nucleus of the carpogenic cell is succeeded by two nuclei, after which the nucleus of the trichophoric cell migrates down close to the carpogonium and undergoes a homoeotypic division. About the same time the septum between the two cells disappears, leaving a long four-nucleated cell. A restored trichophoric cell is then cut off carrying one of the trichophoric daughter nuclei; an inferior supporting cell with one of the two nuclei which succeeded the carpogenic nucleus is cut off below. Four nuclei now appear in place of the two remaining centrally-placed nuclei, and a superior binucleate supporting cell is formed above, leaving a binucleated ascogonium below. The ascogonium may become an ascogenic cell directly, or a second inferior supporting cell may be cut off from it, and a second ascogenic cell may be formed, each cell being binucleate. At this important point the exact line of descent of the nuclei to be found in this series of binucleate cells was not determined. Whether the nuclei in the ascogenic cells are sister nuclei, a few divisions removed from the nucleus of the carpogonium, or whether they are non-sister nuclei, the great-granddaughters of the trichophoric and carpogenic cells respectively, is not stated. The author would seem to infer that the latter is the case by the statement that the nucleus of the trichophoric cell "joins forces with that of the carpogonium." The nuclei in the ascogenic cell divide conjugately, non-sister nuclei passing up into the ascus which buds off directly from the ascogenic cell. Their fusion follows. Four chromosomes appear at the conjugate divisions in the ascogenic cells and the same number is to be found at each division in the ascus; reduction occurs in synapsis of the first division. A well-marked centrosome is found upon the nuclear membrane. The behavior of the centrosome in nuclear division, and its connection with the chromatin threads seems to be very similar to what Harper describes for the Erysiphaceae. Faull still maintains, however, that the astral rays take no part as such in the delimitation of the spores, but agrees that the centrosome is the center of activity to the extent that the spores are delimited by the differentiation of a limiting layer

of protoplasm that begins adjacent to the centrosome and continues progressively.

Faull has procured additional cytological evidence for placing the Laboulbeniales among the true Ascomycetes. It should be noted, however, that the method of ascogonous formation here described is entirely unlike anything known among the ascomycetes. Although he has heretofore been inclined to view the ascus as having been evolved from the zoosporangium of the Oomycetes, he now admits that there may be some grounds for relating the Ascomycetes to the Florideae. "Such features as a uninucleate antheridium, the possibility of proliferation of spermatia from the same antheridium, and the exogenous types of spermatium organization suggest similar phenomena in the rusts, many Ascomycetes, and in the Florideae."

B. O. DODGE.

MAIRE'S REMARKS ON SOME HYPOCREACEAE

Under the title "Remarques sur quelques Hypocréacées"[3] R. Maire discusses a number of species belonging to the genera *Pyxidiophora, Peckiella, Hypomyces,* and *Nectriopsis,* the last being a new genus. In this paper a number of data are given which add to our knowledge of the North American Hypocreales.

In the "Hypocreales of North America"[4] the writer made *Hypomyces boletinus* Peck a synonym of *Hypomyces chrysospermus* (Bull.) Tul. with a note that the spores in the North American specimens examined were smaller than usually indicated for European specimens. On this difference Maire retains the American form as a variety of the European. At the time this note was made it was the opinion of the writer that the difference in size of the spores was due to immaturity of the plants examined. It still seems likely that this apparent difference would fade out if a careful comparison could be made of a sufficient number of plants from both America and Europe. The species is common on *Boletus* but the conidial phase is more common than the perfect and is identical in the European and

[3] Ann. Myc. 9: 315–326. 1911.
[4] MYCOLOGIA 2: 76. 1910.

American plants. The perithecia develop quite readily in the laboratory.

After a study of cotype material of *Hypomyces hyalinus* (Schw.) Tul. in the herbarium at Paris, Maire agrees with the writer in regard to the spore characters, the species being characterized by the unequally septate, verrucose spores. *Hypomyces inaequalis* Peck is used as a synonym as has been previously done by the writer (l. c.). Maire calls attention to the fact that the species has also been recorded from Europe, a fact which was overlooked in our own monograph.[5]

Hypomyces macrosporus Seaver is made a synonym of *Hypomyces armeniacus* Tul. When this species was described a note was appended stating that the plant was first thought to be *Hypomyces ochraceus* (Pers.) Tul. The absence of material illustrating this species in Persoon's herbarium, together with several apparent differences, led me to describe the species as new. Maire points out that it is identical with *Hypomyces armeniacus* Tul. in the Paris herbarium and adds *Hypomyces ochraceus* (Pers.) Tul. as a doubtful synonym. These observations are important as they clear up the identity of our North American species. The species is characterized by the very large verrucose spores.

Specimens of *Hypomyces tegillum* Berk. & Curt. in the herbarium at Kew show perithecia, but no mature asci were seen. Maire reports that cotype material in the Paris herbarium have asci in good condition, and completes the description of the species. *Hypomyces papyraceus* (Ellis & Holw.) Seaver differs in the much smaller spores.

Nectriopsis is proposed as a new genus, differing from *Byssonectria* in its 2-celled spores. *Hypomyces violaceus* Tul., which was placed in the genus *Byssonectria* by the writer, is included in the new genus. *Hypomyces aureo-nitens* Tul. is also included in the new genus. The American material described under this name in NORTH AMERICAN FLORA is said to differ in its much smaller spores and the absence of the *Penicillium*-type of conidia.

The paper is illustrated with one plate containing careful drawings of the spores of the species discussed, and is a valuable addition to our knowledge of the North American Hypocreales.

F. J. SEAVER.

[5] Fries, Summa Veg. Scand. 383. 1849.

WOLLENWEBER'S STUDIES ON THE FUSARIUM PROBLEM

A paper entitled "Studies on the Fusarium Problem," by Dr. H. W. Wollenweber, appears in *Phytopathology* (3: 24–50. 1913). As an introduction to this paper he first discusses "unreliability of the stroma as a taxonomic character" in the ascomycetes. He says in referring to the stroma, "Doubts, however, as to the value of the basis of Fries' system have been frequently expressed." "These doubts have recently been confirmed by careful comparative studies of exsiccati and by pure culture study of ascomycetes and fungi imperfecti." He also says, "This system somewhat modified is still in use." Also, that it will be difficult or almost impossible to follow the proposition to divide the Hypocreales into groups according to the presence or absence of stroma as has been done in NORTH AMERICAN FLORA.

He might have discussed "Unreliability of Any Taxonomic Character" and all of the arguments which have been advanced in support of his ground would apply with equal validity to many if not all of these characters. That the stroma, in certain cases, is variable, has long been recognized by taxonomists, but to argue that divisions should not be made on this character because it is variable *in certain cases* is about as logical as to argue that the animal and plant kingdoms should not be separated because there are certain groups on the border line which at different stages in their life cycle partake of the character of both animal and plant.

If he had said that it is impossible to separate *some* Hypocreales on the presence or absence of stroma, his statement would be more nearly in accord with fact, but to say that the order as a whole cannot be separated on this character is misleading. Before one undertakes to judge as to the value of a character from a taxonomic point of view, he should first take the trouble to look up some of the facts involved. That Dr. Wollenweber did not do this is evident from his own writing, for in referring to the stroma he says, "It may, however, be of taxonomic value in extreme cases when it entirely encloses the perithecia . . . (*Claviceps, Cordyceps, Xylaria*)." If he had had the facts clearly in mind, he would have known that in certain species of both *Xylaria* and *Cordyceps* the perithecia are not immersed but entirely superficial. Again he writes, "Intermediate groups such as the Hypo-

creaceae having free perithecia, or with the latter partly covered by the stroma. . . . " . . . In many of the Hypocreaceae, contrary to his statement, including the genus *Hypocrea* itself and related genera, the perithecia are entirely immersed, in fact are scarcely more than cavities hollowed out of the stroma. In no genus in the whole order is any character more constant and reliable than the stroma in *Hypocrea, Chromocrea, Chromocreopsis, Podostroma* and other related genera. Even in such cases as *Cordyceps,* in which it might appear extreme to one whose knowledge of the genus is limited to one or two species, the stroma is sometimes quite variable. In at least one case, *Cordyceps Cockerellii,* the stroma becomes so changeable and unreliable that it is on the border line between *Cordyceps* and *Ophionectria.* But, as a whole, the genus *Cordyceps* is well defined. If there were no intermediate forms, classification would be no problem.

Again, referring to Maire's work on *Nectriopsis,* he writes, "In pure culture [*Hypomyces*], however, I find apiculi or sharply pointed ends only on young ascospores, with more or less obtuse ends in maturity." The species on which this observation was made is not named. The genus *Hypomyces* was founded by Tulasne (not Plowright) on *Sphaeria Lactifluorum.* This species has been studied by the writer from living material both in the laboratory and field over long stretches of time, involving literally bushels of material and in no case have my observations on the ascospores borne out those of Wollenweber, which leads me to suspect that the peculiar condition observed in his work was due to abnormal conditions or possibly that he did not have a *Hypomyces* at all.

On this latter observation, which is so lacking in detail that it is not conclusive, he rules that the morphology of the ascospore is not a reliable character on which to separate *Hypomyces* and *Nectria.* On even more limited observation he adopts a new character, "true chlamydospores," in which, to use his own words, "we have an excellent differential character between both genera." What reason he has to assume that chlamydospores occur throughout the genus *Hypomyces* and not throughout the genus *Nectria,* since they have been reported in some species of both genera, he does not make clear. If they should later be

found to occur throughout both genera, we cannot understand how their presence or absence could be used as a differential character between the two. If later they should be found to be common to many of the pyrenomycetes, having been already reported in several, we fail to understand how their presence could be of any value as a generic character at all. Then, with our present incomplete knowledge of the nature of, or the conditions under which chlamydospores are formed, what reason have we to believe that they are constant in their occurrence in any given species? Is it not possible that their presence or absence may be even more unreliable than the stroma itself?

On the above outlined uncertain evidence, he adopts the presence or absence of chlamydospores as a differential character between *Nectria* and *Hypomyces* and proposes in order to make the character fit the few species investigated to transpose all the species of *Nectria* in which chlamydospores *have been reported* to the genus *Hypomyces*, and publishes the new combination for *Nectria Ipomoeae* Halsted.

While no line of work is of more value to the taxonomist than life history study of the various species of fungi, yet to attempt to draw general conclusions as to the value of taxonomic characters by an investigation of a few isolated species is not improving classification but only adding chaos to confusion. After thus so easily disposing of most of the difficulties in the classification of the Hypocreales, he then proceeds to record the results of his work on *Fusarium*, in which field he has contributed much valuable knowledge to the cause of science.

The genus *Fusarium* is divided into sections on the basis of the forms of the conidia, as follows: Elegans, Martiella, Discolor, Gibbosum, Roseum, and Ventricosum. The types of conida on which these sections are based are given in an accompanying plate. *Verticillium* is briefly considered, although showing no morphological relationship with *Fusarium*. *Ramularia*, which differs from *Fusarium* in its cylindrical conidia, is also considered.

It is assumed as a general rule that the presence of chlamydospores in certain sections of *Fusarium* indicates the absence of ascogenous stages. There are, however, exceptions in *Hypomyces* and *Nectria*.

The wilt disease is fully discussed. The view which has been previously advanced that *Neocosmospora* is an obligate saprophyte and not connected with *Fusarium vasinfectum* Atk., as has been supposed, is sustained. The question then arises as to the validity of the name *Neocosmospora vasinfecta* Smith, the species having been founded on Atkinson's name given to the *Fusarium*. This illustrates the difficulty, at the present stage of our knowledge, of relying on conidial characters in the classification of the Ascomycetes.

Considerable space is devoted to "Tuber rot and ring discoloration of the potato." According to his investigations, six species of *Fusarium* have been confused with *Fusarium Solani;* also *Hypomyces Solani* and *Nectria Solani,* which have been thought to represent its ascogenous stage and are now regarded as harmless saprophytes. It is claimed that all of these species of *Fusarium* can be distinguished on morphological characters.

This paper contains many valuable suggestions, but, from the standpoint of a taxonomist, it would seem to me that if more space had been used in recording exact details of pure culture experiments on which these conclusions are based and a little less in generalizing on their probable application, its value would have been greatly enhanced, at least so far as our knowledge of the ascomycetes is concerned.

F. J. SEAVER.

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